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Fish Growth: Investigations Based on a Size-Structured Model

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Schnute, J. T., L. J. Richards, and A. J. Cass. 1989. Fish growth: investigations based on a size-structured model. Can. J. Fish. Aquat. Sci. 46: 730–742.

In this paper and its companion (Schnute et al. 1989, Can. J. Fish. Aquat. Sci. 46: 743–769), we present a statistical analysis of Schnute's size-structured model for exploited fish populations. Here we emphasize model parameters associated with fish growth. The model projects the growth of population biomass from the growth of individual fish. We show that this relationship between individual and global behavior is formally analogous with the kinetic theory of gases, where properties of a gas follow from the motions of individual particles. Our statistical analysis allows for error in all observed variables, and we support all analytical arguments with simple graphical techniques. We illustrate the model with tag–recapture and fishery data from an exploited lingcod (*Ophiodon elongatus*) stock. Growth parameter estimates from the population are based on weight means and variances within the catch over the period 1956–86. These estimates agree well with estimates based on weights of individual fish released in 1982 and recaptured in 1983.

Dans cet article et le suivant (Schnute et coll. 1989, Can. J. Fish. Aquat. Sci. 46 : 743–769), nous présentons une analyse statistique du modèle structuré en fonction de la taille de Schnute utilisé pour les populations de poissons exploitées. Dans cet article, nous mettons l'accent sur les paramètres du modèle associés à la croissance des poissons. Le modèle exécute une projection de la croissance de la biomasse d'une population de poissons à partir de la croissance des individus. Nous montrons que cette relation entre le comportement individuel et le comportement collectif est parfaitement analogue à la théorie cinétique des gaz, suivant laquelle les propriétés d'un gaz découlent du mouvement des particules individuelles. Notre analyse statistique tient compte des erreurs dans toutes les variables observées, et nous appuyons tous nos arguments analytiques au moyen de techniques graphiques simples. Nous illustrons le modèle par des données de marquage et de recapture chez une population exploitée de morue–lingue (*Ophiodon elongatus*). Les calculs servant à déterminer la croissance de la population sont effectués à partir du poids moyen (et de sa variance) des poissons capturés entre 1956 et 1986. Ces calculs corroborent les calculs effectués à partir du poids des individus libérés en 1982 et recapturés en 1983.

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Schnute (1987) proposed a size-structured model for exploited fish populations. The model is particularly applicable to cases where catch-at-age data are not available, but the size–frequency distribution of the catch is known. Essentially, the model consists of general population equations that follow from common assumptions about growth, fishing, survival, and recruitment. Schnute (1987) described these equations in an entirely deterministic context. Their practical application to fishery data, however, requires a statistical formulation that leads to estimates and confidence intervals for the unknown parameters.

In this paper and its companion (Schnute et al. 1989), we present statistical versions of the principal equations in Schnute's size-structured model, and we illustrate their application to stock assessment. Not only do we describe parameter estimation methods, but, perhaps more importantly, we show how the model equations can guide logical thinking about the data. Easy graphical methods sometimes suggest crude parameter estimates (and even confidence intervals) that agree remarkably well with the final analytical results. Together, our two papers demonstrate that a well crafted model serves not only as an analytical tool, but also as a conceptual device for illuminating the data's essential features. Since the fishery biologist must often explain his conclusions to fishermen and the general public, a cogent description of the fishery can be as important as the analysis itself.

This paper focuses primarily on fish growth, while the companion paper (Schnute et al. 1989) addresses issues associated with survival and recruitment. An essential feature of Schnute's (1987) model is that population growth is explained on the basis of growth of individual fish. In this respect the model can be compared with the kinetic theory of gases, where dynamic properties of a gas follow directly from the laws of motion of individual molecules. Indeed, there are precise formal comparisons between equations for a size-structured population and results obtained in kinetic theory (Schnute and Shinbrot 1973; Schnute 1976). We give empirical evidence for this result here by comparing the growth of individual tagged fish with the growth of the whole population.

In section 1 of this paper we summarize the main conclusions of Schnute's (1987) size-structure theory, particularly in regard to fish growth. In section 2 we present a statistical model from which we derive formal estimates for the model's growth parameters, based on data either from individual fish or from the population as a whole. In section 3 we describe data collected on a lingcod (*Ophiodon elongatus*) stock, which illustrates the model's application. We show how to compile the data in a manner required by the model and describe a graphical analysis that highlights the data's essential structure in regard

to fish growth. Finally, we develop formal estimates and confidence intervals for the growth parameters, based on the statistical model of section 2. These are used in our second paper, where we continue the analysis by focusing on survival and recruitment.

1. Model Summary

Schnute's (1987) size-structured model is based on three principal assumptions. The first is that, if a fish has weight w at the start of one year, then its weight w' at the start of the next year is determined by the linear growth law

$$(1.1) \quad w' = W + \rho w$$

where the parameters W and ρ represent the intercept and slope, respectively. This equation has been used widely as a descriptor of fish growth, dating back to Ford (1933) and Walford (1946). In (1.1), w can act as a surrogate for a variety of possible size measures. For example, w could represent log–weight in a population where fish follow Gompertz growth (Deriso and Parma 1988). More generally, w could be an exponential transform of weight if fish conform to Schnute's (1981) generalized growth law. Alternatively, w could represent length or an exponential transform of length.

In this paper, we use weight (without transformation) as the measure of size for two reasons connected with our worked example. First, total weight of the catch is explicitly recorded in the fishery, and, second, direct evidence from tagged fish supports (1.1). Following Schnute (1987), we consistently use a prime ($'$) to denote the result of one year's growth. Thus, if u represents a weight, then u' is shorthand for $W + \rho u$.

Schnute's second assumption relates to the density $N(w, t)$ of fish with weight w at the start of year t. Specifically, he assumes that, for every weight interval (w_1, w_2),

$$(1.2) \quad \int_{w_1'}^{w_2'} N(w, t+1)\, dw = \int_{w_1}^{w_2} \tau(w, t)\, N(w, t)\, dw,$$

where $\tau(w, t)$ represents the fraction of fish with weight w that survive from year t to year $t + 1$. The significance of (1.2) can be understood in the light of (1.1). A fish in the weight interval (w_1, w_2) at the start of year t must, if it survives, have a weight in the interval (w_1', w_2') at the start of year $t + 1$. The integral on the left side of (1.2) represents the total number of fish in the interval (w_1', w_2') at the start of year $t + 1$, while the integral on the right represents the total number of survivors from year t with weights in the interval (w_1, w_2). Thus, (1.2) expresses the combined effects of growth and survival from one year to the next, based on summing (i.e. integrating) these effects across weight groups.

Schnute (1987) imposes one restriction on (1.2): the assumption should apply only to fish that are already recruited by year t. He defines recruitment with reference to a specified weight V at which a fish is presumed fully available to the fishery. By (1.1), a fish with weight V at the start of year t will grow to weight V' at the start of year $t + 1$. Any fish in the weight interval (V, V') must be newly recruited to the fishery, since its weight last year was less than V. By contrast, a fish with weight above V' must be previously exploited by the fishery, since it was available to the fishery last year when its weight was V or greater. Thus, (1.2) must be restricted to weight intervals (w_1, w_2) with $w_1 \geq V$. With this constraint, the left-hand integral in (1.2) includes previously exploited fish, which are survivors from year t, and excludes new recruits in year $t + 1$.

Schnute's third assumption is that mortality is not size selective for recruited fish. Mathematically, this is expressed by

$$(1.3) \quad \tau(w, t) = \tau_t \text{ for } w \geq V.$$

In particular, (1.3) is true if neither natural nor fishing mortality is size dependent. Since V is defined as the weight at which a fish is fully available to the fishery, this assumption for the fishing mortality appears to be a reasonable extension of the common assumption that natural mortality is not size dependent.

Assumptions (1.1)–(1.3) are the key ingredients of Schnute's (1987) size-structured model. Further discussion of the Ford–Walford growth law (1.1) is required, however, for the application here. When $0 < \rho < 1$, (1.1) is implied by von Bertalanffy growth

$$(1.4) \quad w(a) = W_\infty [1 - e^{-K(a-a_0)}],$$

where $w(a)$ represents weight at age a and the three parameters W_∞, K, and a_0 determine W and ρ by

$$(1.5a) \quad W = W_\infty (1 - e^{-K}),$$

$$(1.5b) \quad \rho = e^{-K}.$$

Consequently, (1.1) is more general than (1.4), which assumes that a fish of age a must have a specified weight $w(a)$. By contrast, (1.1) asumes only that a weight w determines a subsequent weight w' one year later, regardless of age. Like (1.4), (1.1) implies that fish grow to an asymptotic size W_∞ given by

$$(1.6) \quad W_\infty = \frac{W}{1 - \rho},$$

when $0 \leq \rho < 1$. When $\rho \geq 1$, there is no asymptotic size; however, equations (1.4)–(1.6) remain valid when $\rho > 1$. In this case K is negative, and W_∞ is opposite in sign to W.

The model's application requires dividing the population into two size groups, as discussed above. Newly recruited fish are those with weights in the interval (V, V'), while previously exploited fish have weights in (V', ∞). The total recruited population consists of these two groups combined, that is, fish with weights in (V, ∞). For each group of fish, a variety of population variables at the start of year t can be calculated from $N(w, t)$, such as the number of animals, the total biomass, the average weight, and the variance in weight. Table 1 summarizes notation for the principal quantities of interest here.

Consider, for example, variables associated with the entire recruited population. The total number of recruited fish at the start of year t is the integral

$$(1.7) \quad N_t = \int_V^\infty N(w, t)\, dw,$$

where, incidentally, $N(w, t) = 0$ for $w > W_\infty$ when $\rho < 1$. Similarly, the total recruited biomass at the start of year t is

$$(1.8) \quad N_t^* = \int_V^\infty w\, N(w, t)\, dw,$$

and the average weight per fish is

$$(1.9) \quad X_t = N_t^*/N_t.$$

Weight dispersion is related to the departure of a typical weight w from the mean X_t, i.e. the difference $w - X_t$. In general, the total dispersion of order n at the start of year t is

$$(1.10) \quad N_t^{(n)} = \int_V^\infty (w - X_t)^n\, N(w, t)\, dw,$$

and the average dispersion is

$$(1.11) \quad X_t^{(n)} = N_t^{(n)}/N_t.$$

TABLE 1. Summary of notation for population variables, where each component of the population is defined by the indicated weight interval. Measures of dispersion are associated with an order n (n = 2,3,4,...), where second order dispersion relates to variance.

Quantity	Population component		
	Recruited	Newly recruited	Previously exploited
Weight interval	(V, ∞)	(V, V')	(V', ∞)
Numbers	N_t	R_t	P_t
Biomass	N_t^*	R_t^*	P_t^*
Weight dispersion	$N_t^{(n)}$	$R_t^{(n)}$	$P_t^{(n)}$
Mean weight	X_t	Y_t	Z_t
Mean dispersion	$X_t^{(n)}$	$Y_t^{(n)}$	$Z_t^{(n)}$

Since $X_t^{(2)}$ represents the weight variance, definitions (1.10)–(1.11) have particular biological significance when $n = 2$.

The quantities N_t, N_t^*, X_t, $N_t^{(n)}$, and $X_t^{(n)}$ defined in (1.7)–(1.11) all are associated with the weight interval (V,∞) for the total recruited population. As indicated in Table 1, corresponding quantities R_t, R_t^*, Y_t, $R_t^{(n)}$, and $Y_t^{(n)}$ can be defined for the newly recruited poplation with weights in the interval (V, V'). Thus, R_t, R_t^*, $R_t^{(n)}$ are given by integrals similar to (1.7), (1.8), and (1.10), respectively, with an upper limit V' rather than ∞. Similarly, if X and N are replaced by Y and R, respectively, in (1.9) and (1.11), the resulting equations define Y_t and $Y_t^{(n)}$. Finally, the quantities P_t, P_t^*, Z_t, $P_t^{(n)}$, and $Z_t^{(n)}$ in Table 1 can be defined analogously for the previously exploited population by integrating over the weight interval (V',∞).

With the aid of notation listed in Table 1, it is now possible to state Schnute's (1987) main results. He shows that assumptions (1.1)–(1.3) lead mathematically to the following four conclusions:

$$N_{t+1} = R_{t+1} + \tau_t N_t, \tag{1.12}$$

$$N_{t+1}^* = R_{t+1}^* + \tau_t (X_t'/X_t) N_t^*, \tag{1.13}$$

$$Z_{t+1} = X_t', \tag{1.14}$$

$$Z_{t+1}^{(n)} = \rho^n X_t^{(n)}. \tag{1.15}$$

These have simple biological interpretations. For example, (1.12) states that the population at the start of year $t + 1$ consists of new recruits in that year plus survivors from year t. The result (1.13) corresponds to a similar dynamic equation for the total biomass, except that the biomass N_t^* from year t is multiplied by both a survival factor τ_t and a growth factor X_t'/X_t. Thus, survivors contribute to the subsequent biomass not only because they have survived, but also because they have grown. Since previously exploited fish consist entirely of survivors, their average weight Z_{t+1} in year $t + 1$, as expressed by (1.14), is just the projected value X_t' from the average X_t for the whole population in year t. Furthermore, growth influences weight dispersion. If $\rho < 1$, then small fish grow more rapidly than large fish; consequently, weight dispersion is reduced by growth. Similarly, if $\rho > 1$, large fish grow more rapidly than small fish, and weight dispersion increases. These conclusions are expressed mathematically by (1.15), where the factor ρ^n corresponds to a decrease or increase in dispersion, respectively, when $\rho < 1$ or $\rho > 1$.

Results (1.12)–(1.15) are derived mathematically in Appendix A. The derivations here differ slightly from those in Schnute (1987) by emphasizing formal similarities with the kinetic theory of gases. Biologically, this similarity is most evident in (1.14), which is a population growth law that mirrors the growth law (1.1) for individual fish. Just as laws of motion for particles imply corresponding laws for a gas, so also a growth law for individual fish leads to a corresponding law for the population.

2. Statistics and Parameter Estimation

The discussion so far has focused entirely on deterministic equations. This section develops statistical theory necessary for estimating growth parameters from observed data. Two possible types of data are considered here: (1) weights of individual fish and (2) weight means and variances within the whole population. If a minimum recruitment weight V has been specified, then the growth law (1.1) can be rewritten as

$$w' = V' + \rho(w - V), \tag{2.1a}$$

where, as usual, $V' = W + \rho V$. We impose the constraints

$$\rho \geq 0, \tag{2.1b}$$

$$V' \geq V, \tag{2.1c}$$

on ρ and V' to guarantee that $w' \geq w$ (i.e. fish do not shrink in size) when w is in the admissible size range ($V \leq w \leq W_\infty$ when $\rho < 1$, or $w \geq V$ when $\rho \geq 1$). Note that (2.1) expresses a growth law identical to (1.1), except that the parameters are ρ and V', rather than ρ and W. In (2.1), V is regarded, not as a parameter to be estimated, but rather as a specified quantity.

To avoid possible confusion later, we stress that the constraint (2.1c), connected with growth, differs from the assumption (1.3) that recruitment is knife edged. In (2.1) we use V mainly as a convenient reference weight, relative to which we estimate the parameter V'. It turns out that estimates of V' and ρ tend to be much less correlated than estimates of W and ρ. Since the weight $w = 0$ is outside the range of data, the estimated intercept W (where $w = 0$) is highly sensitive to the estimated slope ρ.

Consider first the problem of estimating ρ and V' from a sample of n fish that have been weighed, tagged, returned to the sea, recovered 1 yr later, and weighed again. The data consist of a set of n pairs (u_i, v_i), where u_i is the weight of the ith fish when it is first tagged and returned to the sea and v_i is the weight of the same fish when it is recovered 1 yr later. The following model provides a statistical counterpart of (2.1) for this data set:

$$u_i = w_i + \alpha\delta_i, \tag{2.2a}$$

$$v_i = w_i' + \alpha\epsilon_i, \tag{2.2b}$$

$$w_i' = V' + \rho(w_i - V), \tag{2.2c}$$

for $i = 1,\ldots, n$. In (2.2) δ_i and ϵ_i are assumed to be independent normally distributed random variables with mean 0 and vari-

ance 1. The parameter α represents a standard deviation associated with statistical error in (2.2). Each parameter w_i ($i = 1,\ldots n$) corresponds to an intrinsic weight for the ith fish such that the pair (w_i, w_i') satisfies the growth law (2.1) exactly. The model (2.2) is an errors-in-variables model because it includes error in both observations u_i and v_i. A key assumption in (2.2) is that the errors associated with u_i and v_i share the same standard deviation α. It is known from general theory (Kendall and Stuart 1979, p. 407–410) that some assumption relating the standard deviations in (2.2a) and (2.2b) is required for maximum likelihood parameter estimation. In this case, because u_i and v_i have the same units of measurement (such as kilograms) and approximately the same order or magnitude, it is reasonable to suppose that they share the same standard deviation in their departure from the line (2.2c).

The model (2.2) involves $3 + n$ parameters: ρ, V', α, and w_i ($i = 1,\ldots n$). In terms of these, the likelihood function for the observed data (u_i, v_i) is the following product of normal probability densities:

$$(2.3)\quad L = \left(\frac{1}{2\pi\alpha^2}\right)^n \exp\left[-\frac{1}{2\alpha^2}\sum_{i=1}^{n}\{[u_i - w_i]^2 + [v_i - V' - \rho(w_i - V)]^2\}\right].$$

Furthermore, for given values of ρ and V', the maximum likelihood estimates for w_i and α^2 turn out (Appendix B) to be

$$(2.4)\quad \hat{w}_i = V + \frac{(u_i - V) + \rho(v_i - V')}{1 + \rho^2},$$

$$(2.5)\quad \hat{\alpha}^2 = \frac{1}{2n(1 + \rho^2)}\sum_{i=1}^{n}[(v_i - V') - \rho(u_i - V)]^2,$$

respectively. These estimates can be substituted into the likelihood function (2.3) to eliminate all parameters except ρ and V'. In fact, if $l(\rho, V')$ is twice the negative log likelihood (except for a constant independent of parameters) evaluated at the estimates (2.4)–(2.5), then it can be shown (Appendix B) that

$$(2.6)\quad l(\rho, V') = 2n \cdot \log\{S_{vv} - 2\rho S_{uv} + \rho^2 S_{uu} + [(\bar{v} - V') - \rho(\bar{u} - V)]^2\} - 2n \cdot \log(1 + \rho^2),$$

where $(\bar{u}, \bar{v})$ represents the usual mean of the data (u_i, v_i), $i = 1,\ldots, n$, and S_{uu}, S_{uv}, and S_{vv} are the sums

$$(2.7a)\quad S_{uu} = \sum_{i=1}^{n}(u_i - \bar{u})^2,$$

$$(2.7b)\quad S_{uv} = \sum_{i=1}^{n}(u_i - \bar{u})(v_i - \bar{v}),$$

$$(2.7c)\quad S_{vv} = \sum_{i=1}^{n}(v_i - \bar{v})^2.$$

The function l in (2.6) depends only on the data and the growth parameters ρ and V'. It serves two purposes here. First the minimum of l defines the maximum likelihood estimates $\hat{\rho}$ and $\hat{V}'$. In this case, it is possible (Appendix B) to obtain the following analytical expressions for these estimates:

$$(2.8)\quad \hat{\rho} = \frac{1}{2S_{uv}}[(S_{vv} - S_{uu}) + ((S_{vv} - S_{uu})^2 + 4S_{uv}^2)^{1/2}],$$

$$(2.9)\quad \hat{V}' = \bar{v} - \hat{\rho}(\bar{u} - V).$$

The second purpose of l is to determine a confidence region for ρ and V' as follows. Let p denote probability level ($0 < p < 1$), and let $\chi^2(2, p)$ be the cutoff at level p for the χ^2 distribution with 2 *df*. Then, an approximate $100 \cdot p\%$ confidence region for ρ and V' is defined by the interior of the curve where

$$(2.10)\quad l(\rho, V') = l(\hat{\rho}, \hat{V}') + \chi^2(2, p). \text{ (see addendum)}$$

The justification for (2.10) comes from the likelihood ratio test (Kendall and Stuart 1979, chapter 24), where $\chi^2(2, p)$ is the increment in l above its minimum $l(\hat{\rho}, \hat{V}')$ at which a parameter pair (ρ, V') can be rejected with confidence $100 \cdot p\%$. We note, however, that methods of inference other than (2.10) have been proposed (Edwards 1972). Recent simulation studies (Donaldson and Schnabel 1987) support the approach taken here.

The statistical model (2.2) and the likelihood analysis presented in (2.3)–(2.10) pertain to weight data from individual fish. We next consider a statistical model for population weight data. Such a model can be implemented if both V and V' are specified, so that the weight interval (V, V') for newly recruited fish is known. Historical size structure data from the fishery can then be used to compile mean weights and variances within the population. For example, X_t can be estimated from the mean weight in year t of all randomly sampled fish with weights V or greater. Similarly, estimates of Y_t and Z_t can be obtained from the mean weights in year t of sampled fish within the weight intervals (V, V') and (V', ∞), respectively. Estimates of variances $X_t^{(2)}$, $Y_t^{(2)}$, and $Z_t^{(2)}$ are likewise obtained from weight variances of sampled fish in the appropriate weight groups. Incidentally, when dividing sampled fish between newly recruited and previously exploited groups, it is necessary to adopt a convention for the size V'. We suggest including fish (if any) of the exact size V' in the previously exploited group.

The data of greatest interest here are X_t, Z_t, $X_t^{(2)}$, and $Z_t^{(2)}$. Furthermore, for reasons explained in the example later, it is desirable to convert variances to standard deviations by taking square roots; thus, define

$$(2.11a)\quad B_t = \sqrt{X_t^{(2)}},$$

$$(2.11b)\quad D_t = \sqrt{Z_t^{(2)}}.$$

If fishery data X_t, Y_t, B_t, and D_t are available for years $t = 1,\ldots, T$, then the following equations define an appropriate statistical model that is comparable with (2.2) and consistent with the general theory developed in section 1:

$$(2.12a)\quad X_t = x_t + \beta\delta_t,$$

$$(2.12b)\quad Z_{t+1} = x_t' + \beta\varepsilon_t,$$

$$(2.12c)\quad x_t' = V' + \rho(x_t - V),$$

$$(2.12d)\quad B_t = b_t + \gamma\zeta_t,$$

$$(2.12e)\quad D_{t+1} = \rho b_t + \gamma\eta_t,$$

for $t = 1,\ldots, T - 1$.

In (2.12) δ_t, ε_t, ζ_t, and η_t are assumed to be independent normal random variables with mean 0 and variance 1. This model has $2 + 2T$ parameters: $\rho, V', \beta, \gamma, x_1, \ldots, x_{T-1}, b_1, \ldots, b_{T-1}$. The rationale for (2.12a–c) is similar to that for (2.2). The parameter β represents a standard deviation associated with a relationship between X_t and Z_{t+1}. If β were 0, the exact relationship would be

$$Z_{t+1} = X_t',$$

that is, the population growth law (1.14) suggested by general theory. Thus, equations (2.12a–c) define a statistical version of (1.14), in which error is contemplated in both variables. For

each year t ($t = 1,\ldots, T-1$), the parameter x_t is defined so that (x_t, x'_t) represents an exact point corresponding to (X_t, Z_{t+1}). Similarly, equations (2.12d–e) define a statistical version of (1.15) when $n = 2$:

$$\sqrt{Z_{t+1}^{(2)}} = \rho \sqrt{X_t^{(2)}},$$

where this equation is obtained by equating the square roots of both sides of (1.15). In (2.12d–e) γ represents a standard deviation of error, and the parameter b_t ($t = 1,\ldots, T-1$) is defined so that $(b_t, \rho b_t)$ corresponds to the observed data point (B_t, D_{t+1}) in which both coordinates include statistical error.

Justification for the statistical model (2.12) is somewhat weaker than that for the earlier model (2.2), where observations (indexed i) apply to individual fish. It seems reasonable to suppose that measurements on different fish are independent. By contrast, in (2.12) the observations (indexed t) occur serially, and thus we might expect correlations among them. Indeed, in our companion paper (Schnute et al. 1989) we show how such correlations result from the combined effects of measurement and process errors. As stated here, (2.12) does not include process error, the result of interannual variability in growth. It turns out in our worked example below, however, that the relatively simple model (2.12) is adequate for the purposes here. In order not to detract from the main points of our argument, we defer discussion of more complex serial models to our companion paper, where they play a crucial role.

The likelihood function for (2.12) is similar to that for (2.2), except that in this case it has two components associated with the two sets of data pairs (X_t, Z_{t+1}) and (B_t, D_{t+1}):

$$(2.13)\quad L = \left(\frac{1}{2\pi\beta^2}\right)^{T-1} \exp\left[-\frac{1}{2\beta^2}\sum_{t=1}^{T-1}\{[X_t - x_t]^2 + [Z_{t+1} - V' - \rho(x_t - V)]^2\}\right] \cdot \left(\frac{1}{2\pi\gamma^2}\right)^{T-1} \exp\left[-\frac{1}{2\gamma^2}\sum_{t=1}^{T-1}\{[B_t - b_t]^2 + [D_{t+1} - \rho b_t]^2\}\right].$$

Furthermore, for given values of ρ and V', the maximum likelihood estimates for x_t, b_t, β^2, and γ^2 turn out (Appendix B) to be

$$(2.14)\quad \hat{x}_t = V + \frac{(X_t - V) + \rho(Z_{t+1} - V')}{1 + \rho^2}$$

$$(2.15)\quad \hat{b}_t = \frac{B_t + \rho D_{t+1}}{1 + \rho^2},$$

$$(2.16)\quad \hat{\beta}^2 = \frac{1}{2(T-1)(1+\rho^2)}\sum_{i=1}^{T-1}[(Z_{t+1} - V') - \rho(X_t - V)]^2,$$

$$(2.17)\quad \hat{\gamma}^2 = \frac{1}{2(T-1)(1+\rho^2)}\sum_{i=1}^{T-1}(D_{t+1} - \rho B_t)^2,$$

respectively.

As in the earlier model for tagged fish, it is possible to express the likelihood in terms of ρ and V' alone by substituting the estimates (2.14)–(2.17) into (2.13). In this case, if $l(\rho, V')$ is twice the negative log likelihood (except for a constant) evaluated at the estimates (2.14)–(2.17), it can be shown (Appendix B) that

$$(2.18)\quad l(\rho, V') = 2(T-1)\cdot\log\{S_{ZZ} - 2\rho S_{XZ} + \rho^2 S_{XX} + [(\bar{Z} - V') - \rho(\bar{X} - V)]^2\} + 2(T-1)\cdot\log(\Sigma_{DD} - 2\rho\Sigma_{BD} + \rho^2\Sigma_{BB}) - 4(T-1)\cdot\log(1+\rho^2).$$

Here $\bar{X}$ refers to the mean of the observations X_t ($t = 1, \ldots, T-1$), and $\bar{Z}$ refers to the mean of Z_t ($t = 2, \ldots, T$). Also, the subscripted quantities S and Σ are defined as the following sums:

$$(2.19a)\quad S_{XX} = \sum_{t=1}^{T-1}(X_t - \bar{X})^2,$$

$$(2.19b)\quad S_{XZ} = \sum_{t=1}^{T-1}(X_t - \bar{X})(Z_{t+1} - \bar{Z}),$$

$$(2.19c)\quad S_{ZZ} = \sum_{t=2}^{T}(Z_t - \bar{Z})^2,$$

$$(2.19d)\quad \Sigma_{BB} = \sum_{t=1}^{T-1} B_t^2,$$

$$(2.19e)\quad \Sigma_{BD} = \sum_{t=1}^{T-1} B_t D_{t+1},$$

$$(2.19f)\quad \Sigma_{DD} = \sum_{t=2}^{T} D_t^2.$$

The likelihood function (2.18) can be used for the same purposes in the context of fishery data as the earlier likelihood (2.6) in the context of data on tagged fish. In particular, the minimum of $l(\rho, V')$ gives estimates for ρ and V', and the criterion (2.10) defines a confidence region for these parameters. One problem with this approach, however, is that it is necessary to know V' in order to compile the data (X_t, Z_t, B_t, D_t) from historical fishery samples. Consequently, (2.18) is used primarily to check that the fishery data are consistent with prior estimates of the growth parameters. In some cases, it may be desirable to iterate the use of (2.18): estimate ρ and V', recompile the fishery data, and reestimate ρ and V'. Another approach would be to treat V' as a fixed quantity and to use (2.18) to estimate ρ alone. These possibilities are discussed further in the next section.

Incidentally, it is not possible to obtain an analytic expression, similar to (2.8) above, for the estimate $\hat{\rho}$ from (2.18). If ρ is specified, however, the maximum likelihood estimate for V' is given by a formula similar to (2.9):

$$(2.20)\quad \hat{V}' = \bar{Z} - \rho(\bar{X} - V).$$

3. Illustrative Example

3A. Data Sources

We illustrate the model with data from a lingcod stock off southwest Vancouver Island, British Columbia, Canada, in Pacific Marine Fisheries Commission (PMFC) Major Area 3C–N. A commercial trawl fishery accounts for most of the lingcod catch in this area, and biological samples from this fishery have been collected since 1956. In addition to the fishery data, research data are available from a lingcod tagging study conducted in Area 3C–N in 1982–83. Length measurements were made at the time of fish release in 1982 and again at the

time of recapture in the fishery in 1983. The analysis here is based on the three data sets listed below:

Data set	Time period
Fishery sample weights	1956–86
Tag release and recovery weights	1982–83
Sample ages and weights	1977–85

A more detailed description of these data sets is presented in Cass et al. (1988).

The biological samples provide information on the length distribution of the commercial trawl catch. Conversions from fish length to fish weight for our analysis are somewhat complex because of the different ways in which fish had been prepared prior to sampling. These conversions, applied to both fishery and tag data, are described in Cass et al. (1988). Dorsal fin rays were also collected from the biological samples to determine age composition, beginning in 1977. The fin-ray method of age determination (Beamish and Chilton 1977) has been partially validated for Area 3C–N lingcod (Cass and Beamish 1983).

Female lingcod tend to be larger than male lingcod at a given age. Between 1956–75, however, lingcod were usually dressed and headed at sea; consequently, landed samples could not be sexed. We deal with this problem by modeling the combined stock of both sexes. During the major period of the fishery, between May–September, sexes are nearly equally mixed in the trawl catch. Hence, we include biological samples in our analysis from the May–September fishery only. In any case, the size-structured model is potentially more robust to sexual size differences than an age-structured model. Even if the sexes obey different von Bertalanffy growth laws (1.4), the corresponding growth laws (1.1) may still be similar.

3B. Estimation of V

As a fist step in data compilation, it is necessary to obtain an estimate of V. Two considerations affect this estimate. Because fishing mortality is presumed independent of fish size, V must be large enough to assure constant gear selectivity. On the other hand, the catch of fish of size less than V is treated as mortality prior to recruitment, rather than fishing mortality. Thus, the choice of V must represent a compromise between a size large enough to exclude partial recruitment and a size small enough to include most of the catch.

In our analysis we estimate V from the weight–frequency distributions of the trawl catch for each year (Table 2), averaged over years to produce a combined distribution for the 1956–86 period (Fig. 1). From inspection of the average distribution in Fig. 1, it appears that full recruitment to the fishery occurs at

TABLE 2. Annual number of lingcod sampled and corresponding tabular histogram for the sample weight–frequency distribution of Area 3C–N lingcod. Each histogram is scaled from 0 to 10, where '.' and '*' represent 0 and 10, respectively. Weight intervals are 0.5 kg, where the first interval covers the range 0.25–0.75 kg and the final interval includes all lingcod of 15.25 kg and greater. One histogram is shown for each year (1956–86), and the final row represents the average over all years, with each year weighted equally.

		Weight (kg) at the interval center																													
Year	No.	1		2		3		4		5		6		7		8		9		10		11		12		13		14		15+	
1956	168	.	.	1	6	*	*	4	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1957	1889	.	.	1	3	8	*	7	*	4	4	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1958	1268	.	1	5	*	*	6	6	9	2	4	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1959	1493	.	.	6	8	*	5	4	4	.	1	2	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1960	1455	.	.	4	9	*	4	4	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1961	3448	.	2	6	8	*	7	5	5	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1962	2687	.	1	9	*	*	7	7	*	3	6	6	5	2	3	1	1	2	1	1	1	.	.	.	.	.	.	.	.	.	.
1963	1095	.	.	3	6	9	7	6	*	4	8	8	7	2	4	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.
1964	2266	.	.	3	7	*	8	8	9	3	4	3	3	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1965	3606	.	.	7	*	*	4	3	4	1	3	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1966	3560	.	.	6	*	*	7	5	5	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1967	2229	.	.	5	7	*	6	7	9	3	4	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1968	767	.	2	*	9	6	4	3	6	1	3	4	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1969	2684	.	.	6	*	*	4	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1970	1667	.	.	3	7	*	6	6	6	1	2	2	1	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
1971	1491	.	.	1	1	4	6	6	*	3	6	4	3	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
1972	572	.	1	5	5	4	3	2	6	3	9	*	*	6	7	3	1	3	1	1	.	1	.	2	.	.	.	.	.	.	.
1973	1682	.	1	8	9	*	6	4	8	2	5	4	6	4	7	4	3	5	1	2	2	1	2	1	1	1	1	1	.	3	
1974	1669	.	1	7	*	*	5	3	4	1	3	3	3	.	2	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.
1975	595	.	2	*	8	6	9	3	4	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1976	860	.	1	3	4	4	9	5	8	6	*	5	3	1	1	.	1	.	.	1	.	1	.	.	.	.	.	.	.	.	.
1977	260	.	.	3	4	5	8	3	9	4	*	*	6	4	3	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1978	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1979	285	.	3	2	8	*	9	2	*	6	7	5	4	5	3	.	4	3	.	1	.	.	.	.	.	.	.	.	.	.	.
1980	587	.	.	3	4	4	*	4	8	3	5	2	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1981	437	.	6	*	5	3	6	3	3	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1982	450	.	1	6	8	*	9	3	5	3	2	2	1	2	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1983	270	.	.	3	8	6	*	5	5	3	4	2	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1984	675	.	1	3	5	6	*	5	6	4	3	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1985	1214	.	4	6	5	4	*	6	9	5	7	5	4	4	2	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.
1986	391	.	1	8	*	7	5	4	4	2	5	4	3	4	1	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.
Total		.	1	7	9	*	9	6	8	3	5	3	3	1	2	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.

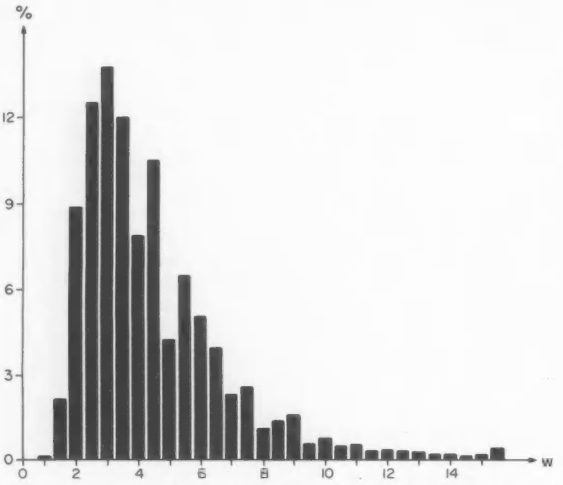

FIG. 1. Percentage of Area 3C–N lingcod in weight category w (kg). Weight categories are defined for 0.5-kg intervals, and the percentages are averaged over the period 1956–86. The final category accounts for all fish within the interval centered on 15.5 kg or larger, i.e. all fish larger than 15.25 kg.

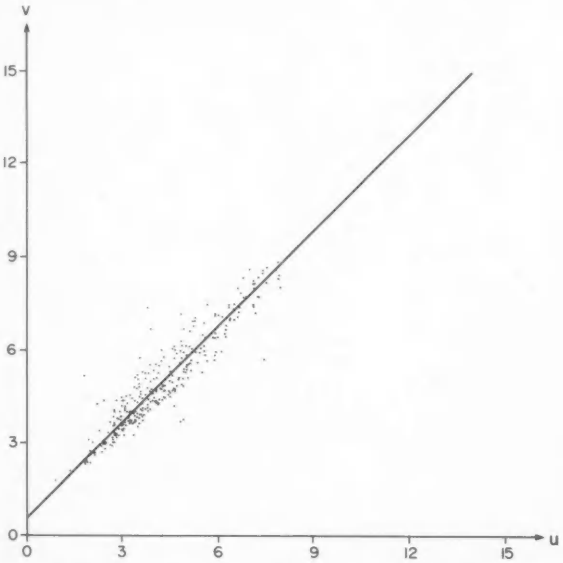

FIG. 2. Release weight u (kg) and recovery weight v for 364 fish released in 1982 and recovered in 1983. The indicated trend line is based on the parameter estimates $\hat{\rho} = 1.025$ and $V' = 2.88$ kg obtained from (2.8)–(2.9) when $V = 2.25$ kg.

a weight in the interval centered on 2.5 or 3.0 kg. These are the two most frequent weight intervals in the distribution. To keep V as a small as possible, subject to the condition of nearly full recruitment, we estimate V to have a value of 2.25 kg, the left end point of the weight interval centered of 2.5 kg. As discussed earlier in connection with (2.1), V serves mainly as a convenient reference weight in the present analysis. In our companion paper (Schnute et al. 1989), where V plays a more

TABLE 3. Parameter estimates from different data sets and models used in the analysis. Three sources of data include aged fishery samples from 1977–85 (Age), a group of tagged fish released in 1982 and recovered in 1983 (Tag), and size–frequency samples from the 1956–86 fishery (Fishery). Models are either a least squares model associated with von Bertalanffy growth (1.4) (VonB) or an errors-in-variables model (EV) based on the Ford-Walford growth law (1.1). The latter was used through three iterations (iter#1, etc.) in an attempt to estimate V' from fishery data. An alternative approach is to use a fixed V' to estimate ρ from the fishery data. Both of these approaches were abandoned in favor of the estimates from the tag data. The tag data with fixed V' illustrates the result for an extreme case.

Data set	Model	W	ρ	V	V'
Age	VonB	0.628	1.043	2.25	2.98
Tag	EV	0.569	1.025	2.25	2.88
Tag	EV: fixed V'	1.034	1.024	2.25	3.50
Fishery	EV: iter#1	0.485	1.011	2.25	2.76
Fishery	EV: iter#2	0.340	1.014	2.25	2.62
Fishery	EV: iter#3	0.211	1.016	2.25	2.50
Fishery	EV: fixed V'	0.646	0.991	2.25	2.88
Fishery	EV: fixed V'	1.327	0.966	2.25	3.50

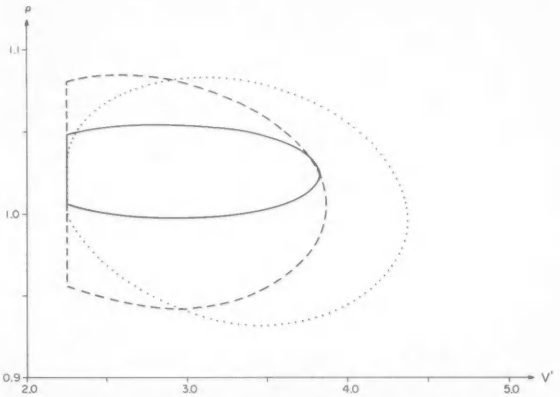

FIG. 3. Approximate 95% confidence regions for ρ and V' (kg) from (2.10), based on tag data (solid curve) and fishery data compiled with $V' = 2.88$ kg (broken curve) and $V' = 3.50$ kg (dotted curve).

significant role, we examine further the implications of this compromise choice for V.

3C. Tag Data Analysis

By applying (2.2)–(2.10) to data from the tagging experiment, estimates and confidence regions for ρ and V' can be obtained. Here, u_i represents the weight of the ith fish sampled at release in 1982, and v_i represents the corresponding weight at recapture in 1983 (Fig. 2). Estimates of ρ and V' (Table 3) are given by (2.8)–(2.9), and a 95% confidence region (Fig. 3) is defined by (2.10). Within this region, ρ varies only slightly from 0.997 to 1.054; consequently, ρ appears to be well defined by the model. By contrast, V', which varies from 2.25 to 3.83 kg, is defined with less precision. Notice, incidentally, that the left side of the confidence region is flat where V' takes the minimum value $V = 2.25$ kg, as required by the constraint (2.1c). Again, we note that this feature is due only to a growth requirement: fish do not shrink in size. The assumption (1.3) that fishing mortality is independent of size does not enter our model for the tagged fish.

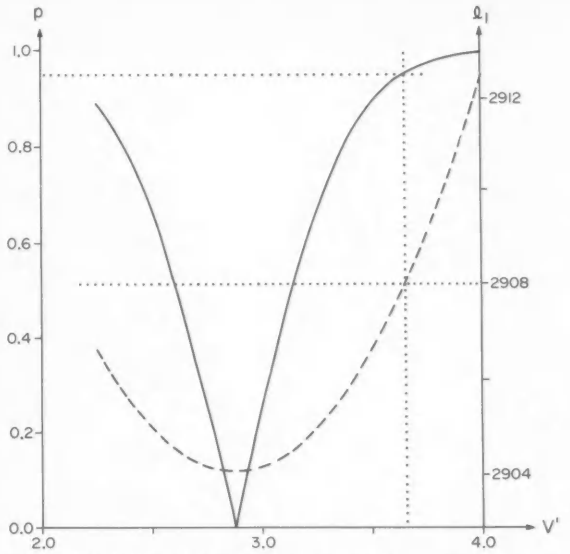

FIG. 4. The likelihood function $l_1(V')$ (broken curve) from (2.6) and (3.1), along with the corresponding probability profile $p(V')$ (solid curve) defined from (3.2). The vertical dotted line indicates the upper end point $V' = 3.64$ kg of a 95% confidence interval for V'. The two horizontal dotted lines show that this value of V' is defined by (3.3) or by the condition that $p = .95$.

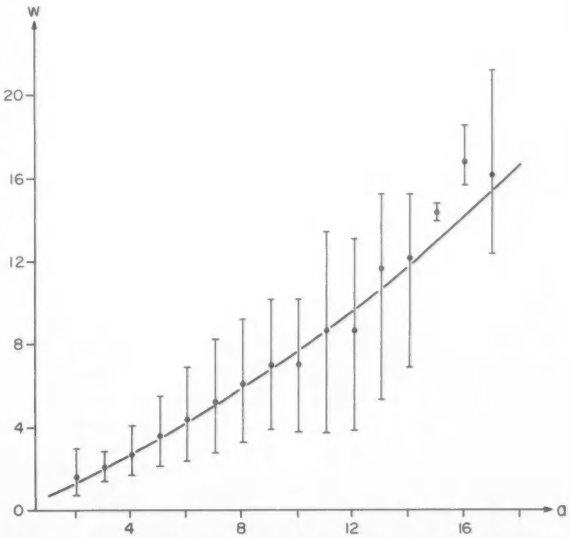

FIG. 5. Mean weight w (kg) at age a (yr), along with fifth and ninety-fifth percentiles of the age–weight distribution, from Area 3C–N lingcod samples taken during 1977–85. The indicated von Bertalanffy growth curve is based on least-squares estimates from (1.4).

Another approach to examining confidence in V' is to determine a probability level associated with various values of V'. Define

$$(3.1)\quad l_1(V') = \min_{\rho} l(\rho, V')$$

for $V' > V$, so that $l_1(V')$ is the lowest possible value of $l(\rho, V')$ in (2.6), given V'. The function $l_1(V')$ is shown as the broken curve in Fig. 4 and has a minimum at $l_1 = 2904.14$, where $V' = 2.88$ kg.

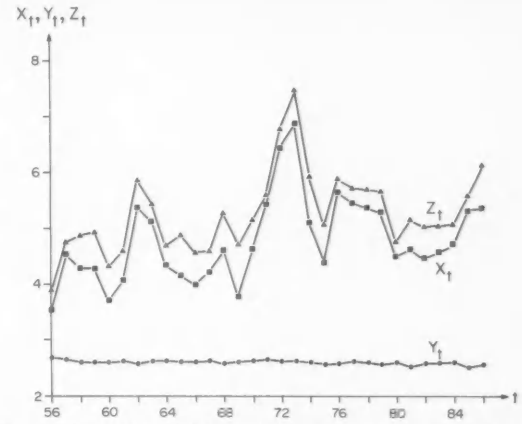

FIG. 6. Time series of the population means X_t, Y_t, and Z_t (kg) for fishery data compiled with $V = 2.25$ kg and $V' = 2.88$ kg. The year t is indicated by two digits so that, for example, "60" refers to 1960.

The end points of an approximate $100 \cdot p\%$ confidence interval for V' are defined by

$$(3.2)\quad l_1(V') = l_1(\hat{V}') + \chi^2(1, p), \text{ (see addendum)}$$

where (3.2), like (2.10), is justified by a likelihood ratio test (Kendall and Stuart 1979, chapter 24). Here 1 *df* is associated with the degree of freedom in the single parameter V', as opposed to 2 *df* in (2.10). The concept underlying (3.2) can be reversed. It is possible to solve for p in (3.2), given $l_1(V')$ and $l_1(\hat{V}')$. The solid curve in Fig. 4 represents these p-levels for the corresponding values of V'. We refer to such a p-level plot as a "probability profile" for the parameter. The profile in Fig. 4 has a typical shape, like a letter "V" that widens at the top. In general, this widening indicates that confidence intervals become broader as p approaches 100%. Similar curves occur in a wide variety of contexts, such as profiles for parameters of the Schaefer model (Schnute 1989). As in our discussion of (2.10), however, we note that methods of inference other than (3.2) have been proposed (Edwards 1972).

To illustrate the use of Fig. 4, consider the problem of finding a 95% confidence interval for V'. By (3.2), an extreme value of V' occurs when $l_1(V')$ is $\chi^2(1, 0.95)$ units above the minimum, that is, when

$$(3.3)\quad l_1(V') = 2904.14 + 3.84 = 2907.98.$$

The figure shows that (3.3) determines the value $V' = 3.64$ kg, where it is also true that $p = 0.95$. Consequently, a 95% confidence interval for V' is

$$(3.4)\quad (2.25 \text{ kg}, 3.64 \text{ kg}),$$

where the lower end point is determined by condition (2.1c). This interval is somewhat narrower than the interval

$$(3.5)\quad (2.25\text{kg}, 3.83 \text{ kg})$$

obtained from the range of values V' within the confidence region in Fig. 3. The distinction between these two intervals is that (3.4) applies irrespective of the value of ρ, while (3.5) comes from a confidence region for ρ and V' combined. Thus, (3.4) better represents a measure of confidence in V', when V' is considered the single parameter of greatest interest.

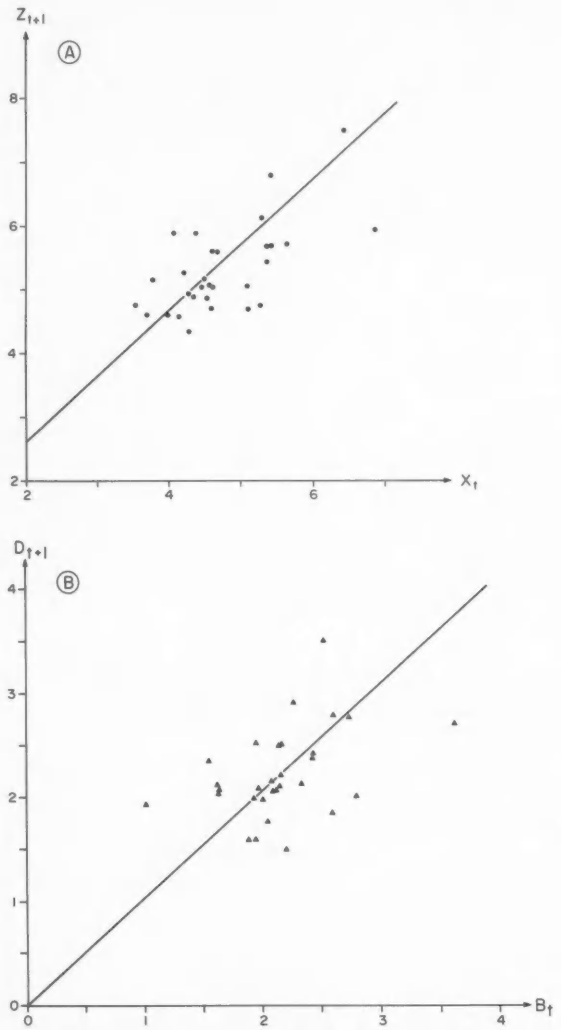

FIG. 7. Scatter plot of the relationship between (A) the means Z_{t+1} and X_t (kg), and (B) the standard deviations D_{t+1} and B_t (kg) for fishery data compiled with $V = 2.25$ kg and $V' = 2.88$ kg, respectively. The indicated trend lines are based on parameter estimates from the tag data in Fig. 2.

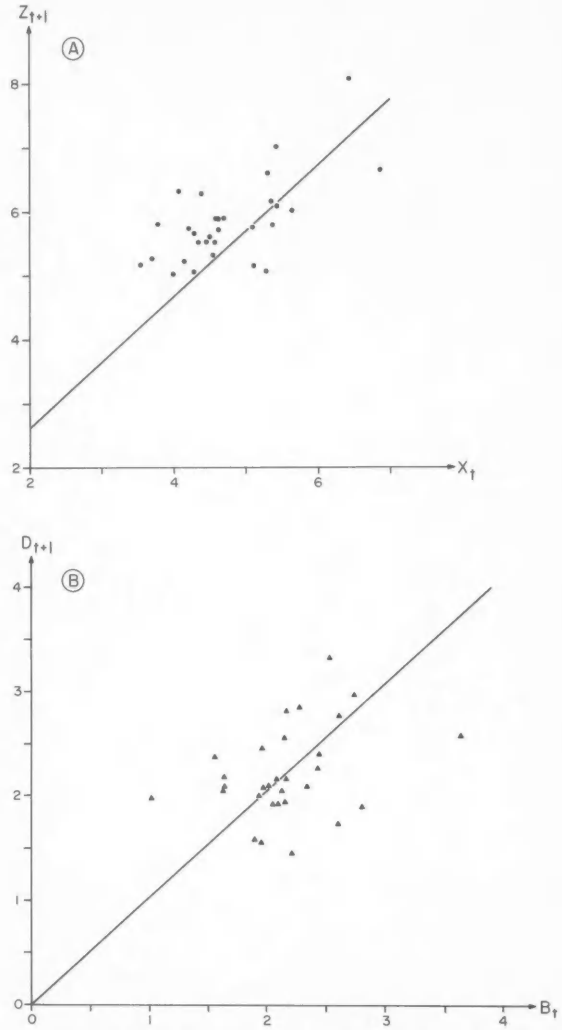

FIG. 8. Scatter plot of the relationship between (A) the means Z_{t+1} and X_t (kg), and (B) the standard deviations D_{t+1} and B_t (kg) for fishery data compiled with $V = 2.25$ kg and $V' = 3.50$ kg, respectively. The indicated trend lines are based on parameter estimates from the tag data in Fig. 2.

3D. Fishery Age Data Analysis

Because both age and weight data are available for some of the biological samples, it is possible to estimate the von Bertalanffy growth parameters in (1.4). For this analysis, the data from 1977–85 are combined across years without regard for possible among-year differences in growth (Fig. 5). Ages of lingcod caught in the fishery range from 2–17 yr. Least squares estimates of the von Bertalanffy growth parameters are $W_\infty = -14.56$, $K = -0.0422$, and $a_0 = -0.1349$. Corresponding estimates of W, ρ, and V' (Table 3) are obtained from (1.5) and (1.1). Incidentally, as discussed earlier in connection with (1.4)–(1.6), notice that both W_∞ and K are negative when $\rho > 1$ and $W > 0$.

Table 3 shows that the estimates of ρ and V' obtained from tagged fish in 1982–83 compare favorably with estimates from aged fishery samples in 1977–85. In our analysis, however, we adopt the estimates from tag data for two reasons. First, the errors-in-variables approach in (2.2) provides a realistic model of statistical error. By contrast, least squares estimation from (1.4) does not allow for ageing error. Second, the tag data correspond specifically to the growth model (1.1), while the age data apply only to the more restrictive model (1.4).

Where possible in this paper and its companion (Schnute et al. 1989), we compare results obtained from different points of view. The size-structured model provides a theoretical link whereby comparison is possible. Thus, for example, we regard the analysis from age data as a confirmation of our results from tag data. Considering the different methods and time periods

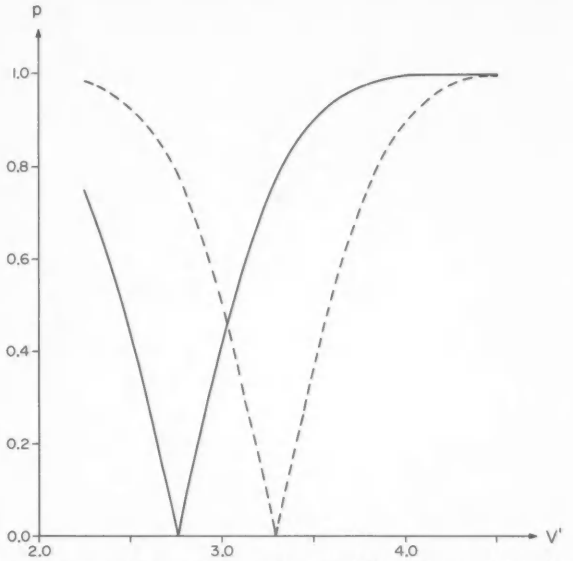

FIG. 9. Probability profiles $p(V')$ from the fishery data compiled with $V' = 2.88$ kg (solid) and $V' = 3.50$ kg (broken).

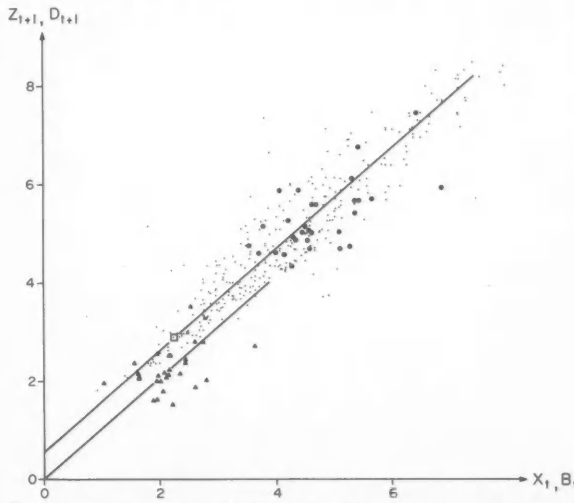

FIG. 10. Composite figure including both fishery and tag data, where the axes have weight units (kg). Circles and triangles indicate, respectively, the points (X_t, Z_{t+1}) and (B_t, D_{t+1}) from the fishery data compiled with $V' = 2.88$ kg. Release and recovery weight pairs (u, v) from Fig. 2 are designated with small dots, where possible on the scale of this figure. A square designates the point (V, V'). The indicated trend lines are based on estimates from the tag data in Fig. 2.

involved in these two data sets, the favorable comparison is encouraging.

3E. Fishery Size Data Analysis

So far we have estimated $V = 2.25$ kg from the size–frequency data in Fig. 1 and $V' = 2.88$ kg from the tag data in Fig. 2. With these estimates for V and V', sample weight data from the fishery can be compiled into three groups associated with the intervals (V, V'), (V', ∞), and (V, ∞). These define the newly recruited, previously exploited, and total recruited populations, respectively. Mean weights X_t, Y_t, and Z_t and weight variances $X_t^{(2)}$, $Y_t^{(2)}$, and $Z_t^{(2)}$ can then be computed for each group from the fish sampled in year t. Fig. 6 shows that the mean weights Z_t and X_t for the previously exploited and total recruited populations, respectively, have tended to increase over the time period 1956–86. Conversely, the series Y_t for the newly recruited population has tended to decrease slightly, although this result is less meaningful due to the relatively small size of the weight interval (V, V').

By (2.12a)–(c), the scatter plot relating Z_{t+1} to X_t for the fishery data (Fig. 7a) is analogous to Fig. 2 for the tag data. It should suggest a line through the point (V, V') with slope ρ. Similarly, by (2.12d)–(e), the scatter plot relating D_{t+1} to B_t (Fig. 7b) should suggest a line of slope ρ constrained through the origin. Lines obtained from the tag estimates of ρ and V' appear to pass reasonably through the fishery data in Fig. 7, although this favorable conclusion is possibly influenced by the estimate of V' used to compile the fishery data. To examine the effect of a different choice of V', we obtain the mean weights and standard deviations for fishery data compiled with $V' = 3.50$ kg. This is a convenient value that corresponds approximately to a p-level of 0.9 in Fig. 4. The appropriate line obtained from tag estimates no longer appears to pass reasonably through the fishery means (Fig. 8a), although the corresponding line constrained through the origin does appear to pass through the standard deviations (Fig. 8b).

Schnute (1987) had suggested that estimates of ρ could be checked from scatter plots of the variances and third moments. We attempted his approach but found the variance about the slope to be more nearly homoscedastic with the transformations (2.11) to standard deviations. There is a similar result for the cube roots of the third moments. As plots of the cube roots of the third moments did not appear to add extra information, we have not included third moments in the present analysis.

Estimates and confidence regions for ρ and V' from the fishery data can be obtained by (2.18) and (2.10). In this case, nonlinear estimation is required, and we apply the simplex search method (Nelder and Mead 1965; Press et al. 1986, p. 289–293), as implemented by Mittertreiner and Schnute (1985). If the data are compiled twice with $V' = 2.88$ kg and $V' = 3.50$ kg, then 95% confidence regions for ρ and V' are as shown in Fig. 3. Both ρ and V' are less well defined by the fishery data than by the tag data. Furthermore, when the fishery data are compiled with $V' = 3.50$ kg, the confidence region includes a wider range of values of V' than when the data are compiled with $V' = 2.88$ kg. Similar patterns for V' are evident in the probability profiles (Fig. 9) obtained from the fishery data by (3.1)–(3.2). These two profiles have similar shapes, but differ in estimates for V'. In both cases, $\hat{V}'$ is lower than the value of V' used to compile the data.

As explained in section 2, (2.18) is used primarily to check that fishery data are consistent with prior estimates of the growth parameters, obtained here from the tag data. As $\hat{V}'$ from (2.18) is lower than V' used to compile the data, we can recompile the data using $V' = \hat{V}'$ and reestimate $\hat{V}'$. The results of three such iterations beginning with $V' = 2.88$ kg are shown in Table 3. In each case, $\hat{V}'$ is lower than the value of V' used to compile the data. In fact, $\hat{V}'$ converges to V. Such a result is clearly unrealistic, as it implies that fish do not grow.

An alternative approach suggested in section 2 is to treat V' as a fixed quantity and to use (2.18) to estimate ρ alone. The results of this approach are shown in Table 3 for $V' = 2.88$ kg

and $V' = 3.50$ kg. In both cases, the estimate for ρ is below the lower 95% confidence region obtained from the tag data, although the difference is small for $V' = 2.88$ kg. Lines drawn using these estimates of ρ and V' pass reasonably through the tag data for $V' = 2.88$ kg; however, for $V' = 3.50$ kg, most tag data points lie below the line.

We finally reject both approaches to estimation from fishery data in favor of accepting the estimates

$$(3.6) \quad \hat{\rho} = 1.025, \hat{V}' = 2.88 \text{ kg},$$

obtained from the tag data by (2.8)–(2.9). We note that the von Bertalanffy estimates, as well as the fishery estimates from (2.18) with $V' = 2.88$ kg and $V' = 3.50$ kg, lie within the confidence region (2.10) from the tag data (Table 3 and Fig. 3). Analysis in our companion paper (Schnute et al. 1989) is based primarily on the estimates (3.6). To examine the consequences of an extreme value of V', we also use the estimates

$$(3.7) \quad \hat{\rho} = 1.024, \hat{V}' = 3.50 \text{ kg},$$

obtained from the tag data by constraining V' at 3.50 kg.

A final composite figure (Fig. 10) illustrates two key features of our analysis: (1) the high degree of consistency between the fishery and tag data sets and (2) the significance of our analogy with the kinetic theory of gases. The tag data represent a single group of fish, released in 1982 and recovered in 1983. The fishery data come from samples collected over the 31-yr period, 1956–86. Both the tag data and the fishery means share a trend line of slope ρ through the point (V, V'). The fishery standard deviations have a parallel trend line through the origin. Thus, the figure provides empirical verification for the lingcod stock that individual and global behavior are linked in a manner consistent with the theory developed here. Single fish, like molecules in a gas, establish a pattern for the whole.

Acknowledgements

We dedicate this paper to the memory of M. Shinbrot, who died prematurely on September 18, 1987. His enthusiastic search for mathematical truth deeply touched professionals in a wide variety of fields. In particular, his work in kinetic theory inspired the analogies developed here.

Addendum

While this paper was being prepared for publication, we conducted further research into confidence intervals associated with errors-in-variables models. Improved estimates can be obtained from counterparts of (2.10) and (3.2), in which an F-statistic replaces the χ^2-statistic used here. We refer interested readers to: SCHNUTE, J. T., T. J. MULLIGAN, AND B. R. KUHN. Analysis of bias from salmon tagging data using an errors-in-variables model. Can. J. Fish. Aquat. Sci. (In press)

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Appendix A. Derivation of Model Equations

This appendix provides derivations of the model equations (1.12)–(1.15). Although these are proved by Schnute (1987), the proofs are repeated here to emphasize analogies with kinetic theory. Fundamental to that theory is the concept of the *state* of a molecule (Schnute 1976, p. 1275) with regard to its position and momentum. The basic axiom of the theory, called *conservation of probability* (op. cit., equation 2.11), relates the motions of individual molecules with an overall probability density function for the gas. This relationship is expressed in terms of integrals across possible states, which vary with time in a manner consistent with the motion of individual molecules.

In the population theory here, the state of a fish is its weight w. The basic axiom (1.2) relates the growth of individual fish to an overall density function for the population. As in kinetic theory, this relationship involves integrals across possible states, i.e. weight intervals, which vary with time t in a manner consistent with fish growth. Thus, the interval (w_1, w_2) transforms to (w_1', w_2') as a result of one year's growth.

In kinetic theory, the first theoretical step involves deriving a differential counterpart of the basic axiom. An analogous step is possible here. Notice that, if w_1 is close to w_2, then (1.2) implies the approximation

$$(A.1) \quad N(w_1', t + 1) \frac{w_2' - w_1'}{w_2 - w_1} \simeq \tau(w_1, t) N(w_1, t).$$

As w_2 tends to w_1, (A.1) tends to the exact equation

$$(A.2) \quad N(w', t + 1) \frac{dw'}{dw} = \tau(w, t) N(w, t),$$

where the subscript on w_1 is dropped for simplicity. This equation is the counterpart of the *Liouville equation* in kinetic theory (op. cit., equation 2.13). The derivative dw'/dw in (A.2) is the Jacobian of the transformation $w \rightarrow w'$. It corresponds to a

similar Jacobian in the Liouville equation, related to expansions or contractions in state space due to the motion of molecules. By (1.1), the Jacobian in (A.2) is simply

$$\text{(A.3)} \quad \frac{dw'}{dw} = \rho.$$

For example, when $\rho < 1$, fish growth is asymptotic. As a result, the weight difference between two fish is reduced with each year of growth. In the language of kinetic theory, growth causes a contraction of state space, and, consequently, the Jacobian (A.3) is less than 1.

Proofs of the principal results depend slightly on whether or not $\rho < 1$. To be specific, we assume in the remainder of this appendix that $\rho < 1$, so that a positive asymptotic weight W_∞ is given by (1.6). In this case fish have weights only in the range (V, W_∞), and $N(w, t) = 0$ when $w > W_\infty$. Furthermore, it can be shown from (1.1) and (1.6) that $W'_\infty = W_\infty$; thus, a fish that reaches the asymptotic weight does not grow beyond it. Mathematically, the proofs below remain valid when $\rho \geq 1$, provided that W_∞ is replaced by ∞.

In kinetic theory, various conservation laws are obtained by multiplying the Liouville equation by simple state functions and integrating over all possible states. In the present context, the simplest analogue of this process results from integrating (A.2) over the entire weight range (V, W_∞). This gives

$$\text{(A.4)} \quad \int_V^{W_\infty} N(w', t + 1) \frac{dw'}{dw}\, dw = \tau_t \int_V^{W_\infty} N(w, t)\, dw,$$

where we use the assumption (1.3) that $\tau(w, t)$ is independent of t. From (1.7), the integral on the right side of (A.4) is simply N_t. Furthermore, because

$$\text{(A.5)} \quad \frac{dw'}{dw}\, dw = dw',$$

the variable of integration on the left side of (A.4) can be transformed to w'. Since this transforms the range (V, W_∞) to (V', W'_∞) and since $W'_\infty = W_\infty$, (A.4) becomes

$$\text{(A.6)} \quad \int_{V'}^{W_\infty} N(w', t + 1)\, dw' = \tau_t N_t.$$

Finally, since the integral in (A.6) is simply $N_{t+1} - R_{t+1}$, we obtain the conservation law

$$\text{(A.7)} \quad N_{t+1} - R_{t+1} = \tau_t N_t.$$

This proves (1.12). Notice in (A.5) that the Jacobian dw'/dw makes the transformation from w to w' straightforward. In kinetic theory, Jacobians play a similar role.

The result (A.7) is the simplest possible conservation law because it results from multiplying (A.2) by 1 and integrating. The analogy with kinetic theory suggests that other laws can be obtained by using various state functions as multipliers. For example, multiplying (A.2) by w' and integrating gives

$$\text{(A.8)} \quad \int_V^{W_\infty} w' \cdot N(w', t + 1) \frac{dw'}{dw}\, dw = \tau_t \int_V^{W_\infty} (W + \rho w) \cdot N(w, t)\, dw,$$

where the expression (1.1) is used for w' on the right. This reduces to the conservation law

$$\text{(A.9)} \quad N^*_{t+1} - R^*_{t+1} = \tau_t(WN_t + \rho N^*_t),$$

where the integral on the left of (A.8) is simplified by logic similar to (A.5)–(A.7).

The law (A.9) takes a more meaningful form biologically if an expression on the right is simplified as follows:

$$WN_t + \rho N^*_t = \left(\frac{W}{X_t} + \rho\right) N^*_t = \frac{W + \rho X_t}{X_t} N^*_t = \frac{X'_t}{X_t} N^*_t.$$

Thus, (A.9) is equivalent to

$$\text{(A.10)} \quad N^*_{t+1} - R^*_{t+1} = \tau_t(X'_t/X_t)N^*_t,$$

which proves (1.13). Furthermore, dividing (A.10) by (A.7) gives

$$\frac{P^*_{t+1}}{P_{t+1}} = \frac{X'_t}{X_t} \cdot \frac{N^*_t}{N_t},$$

based on the definitions of P_t and P^*_t (Table 1). Consequently,

$$Z_{t+1} = (X'_t/X_t)\, X_t = X'_t,$$

and this proves (1.14).

Our final conservation law follows from (A.2) after multiplication by the factor

$$\text{(A.10a)} \quad (w' - Z_{t+1})^n = (w' - X'_t)^n$$

$$\text{(A.10b)} \quad = \rho^n(w - X_t)^n,$$

where (A.10a) and (A.10b) follow from (1.14) and (1.1), respectively. The use of this factor, then, gives

$$\text{(A.11)} \quad \int_V^{W_\infty} (w' - Z_{t+1})^n N(w', t + 1) \frac{dw'}{dw}\, dw = \tau_t \rho^n \int_V^{W_\infty} (w - X_t)^n N(w, t)\, dw.$$

By logic similar to that applied in (A.4) and (A.8), (A.11) implies the law

$$\text{(A.12)} \quad P^{(n)}_{t+1} = \tau_t \rho^n N^{(n)}_t.$$

Dividing (A.12) by (A.7) gives (1.15) and completes the proof of model equations applied in this paper.

Appendix B. Likelihood Estimates

This appendix derives results associated with the likelihood functions (2.3) and (2.13). The proofs are simplified somewhat by use of the notation

$$\text{(B.1)} \quad \tilde{w} = V + \frac{w - V'}{\rho}$$

to indicate the result of projecting the growth law (2.1) backward 1 yr. It follows from (B.1) and (2.1) that

$$\text{(B.2)} \quad (\tilde{w})' = w,$$

that is, $\tilde{w}$ is the weight that will grow to w within 1 yr.

We begin our discussion with the likelihood function L defined in (2.3). Let

$$\text{(B.3)} \quad l_1 = -2 \cdot \log(L).$$

It follows that

$$\text{(B.4)} \quad l_1 = 2n \cdot \log(2\pi\alpha^2) + \frac{1}{\alpha^2} S,$$

where

$$S = \sum_{i=1}^{n} [(w_i - u_i)^2 + (w_i' - v_i)^2]. \quad \text{(B.5)}$$

The derivative condition $\partial l_1/\partial\alpha = 0$ leads to the estimate

$$\hat{\alpha}^2 = S/(2n). \quad \text{(B.6)}$$

Furthermore, evaluating l_1 at $\hat{\alpha}$ gives

$$l_1(\hat{\alpha}) = 2n \cdot \log(\pi e/n) + l_2, \quad \text{(B.7)}$$

where

$$l_2 = 2n \cdot \log(S). \quad \text{(B.8)}$$

The function l_2 is essentially twice the negative log likelihood, except that α has been eliminated in favor of the estimate $\hat{\alpha}$. Thus, l_2 depends only on the remaining parameters ρ, V', and w_i $(i = 1,\ldots,n)$. The condition $\partial l_2/\partial w_i = 0$ gives the following equation for $\hat{w}_i$:

$$\hat{w}_i - u_i = -\rho(\hat{w}_i' - v_i). \quad \text{(B.9)}$$

After some algebra, (B.9) leads to the estimate

$$\hat{w}_i = \frac{u_i + \rho^2 \tilde{v}_i}{1 + \rho^2}. \quad \text{(B.10)}$$

Thus, the estimated true release weight $\hat{w}_i$ is a weighted average of the observed release weight u_i and a weight $\tilde{v}_i$ that results from projecting the observed recovery weight backward 1 yr. This proves (2.4), which is algebraically equivalent to (B.10).

From results derived so far, it can be shown that S in (B.5) evaluated at $\hat{w}_i$ $(i = 1,\ldots,n)$ is

$$S(\hat{w}_1,\ldots,\hat{w}_n) = (1 + \rho^{-2}) \sum_{i=1}^{n} (\hat{w}_i - u_i)^2 \quad \text{(B.11a)}$$

$$= \frac{\rho^2}{1 + \rho^2} \sum_{i=1}^{n} (\tilde{v}_i - u_i)^2 \quad \text{(B.11b)}$$

$$= \frac{1}{1 + \rho^2} \sum_{i=1}^{n} [(v_i - V') - \rho(u_i - V)]^2, \quad \text{(B.11c)}$$

where (B.11a)–(c) follow from (B.9), (B.10), and (B.1), respectively. Combining (B.6) and (B.11c) proves (2.5). Furthermore, if $l(\rho, V')$ is defined by

$$l(\rho, V') = l_2(\rho, V', \hat{w}_1,\ldots,\hat{w}_2), \quad \text{(B.12)}$$

then (B.8), (B.11c), and (B.12) imply (2.6). The essential detail in this proof is to employ the identity

$$(v_i - V') - \rho(u_i - V) = (v_i - \tilde{v}) - \rho(u_i - \tilde{u}) + [\tilde{v} - V' - \rho(\tilde{u} - V)] \quad \text{(B.13)}$$

when computing the sum of squares (B.11c). This completes the proof of results (2.4)–(2.6) associated with the likelihood function (2.3).

From (2.6), it is a relatively straightforward matter to obtain the estimates (2.8)–(2.9). These result from solving the equations $\partial l/\partial V' = 0$ and $\partial l/\partial\rho = 0$ for V' and ρ. The first equation reduces to one that is linear in V', and the second leads to a quadratic equation in ρ. Thus, the only essential difficulty in solving these two equations for V' and ρ is the verification that the root of the quadratic given by (2.8) corresponds to a minimum of l. We leave this as an exercise for the reader, with the comment that the other root corresponds to a maximum.

Proofs associated with the likelihood (2.13) are similar. Again, let

$$l_1 = -2 \cdot \log(L),$$

and notice that

$$l_1 = 2(T-1) \cdot \log(2\pi\beta^2) + \frac{1}{\beta^2} S_1 + 2(T-1) \cdot \log(2\pi\gamma^2) + \frac{1}{\gamma^2} S_2,$$

where

$$S_1 = \sum_{t=1}^{T-1} [(X_t - x_t)^2 + (Z_{t+1} - x_t')^2], \quad \text{(B.14a)}$$

$$S_2 = \sum_{t=1}^{T-1} [(B_t - b_t)^2 + (D_{t+1} - b_t')^2]. \quad \text{(B.14b)}$$

The derivative conditions $\partial l_1/\partial\beta = 0$ and $\partial l_1/\partial\gamma = 0$ lead to the estimates

$$\hat{\beta}^2 = S_1/[2(T-1)], \quad \text{(B.15a)}$$

$$\hat{\gamma}^2 = S_2/[2(T-1)]. \quad \text{(B.15b)}$$

Evaluating l_1 at $\hat{\beta}$ and $\hat{\gamma}$ gives

$$l_1(\hat{\beta}, \hat{\gamma}) = 4(T-1) \cdot \log[\pi e/(T-1)] + l_2,$$

where

$$l_2 = 2(T-1) \cdot [\log(S_1) + \log(S_2)]. \quad \text{(B.16)}$$

By logic similar to that for (B.9), the conditions $2l_2/\partial x_t = 0$ and $\partial l_2/\partial b_t = 0$ imply that $\hat{x}_t$ and $\hat{b}_t$ satisfy

$$\hat{x}_t - X_t = -\rho(\hat{x}_t' - Z_{t+1}), \quad \text{(B.17a)}$$

$$\hat{b}_t - B_t = -\rho(\hat{b}_t' - D_{t+1}). \quad \text{(B.17b)}$$

These lead, in turn, to the estimates

$$\hat{x}_t = \frac{X_t + \rho^2 \tilde{Z}_{t+1}}{1 + \rho^2}, \quad \text{(B.18a)}$$

$$\hat{b}_t = \frac{B_t + \rho D_{t+1}}{1 + \rho^2}. \quad \text{(B.18b)}$$

The results (B.18a)–(b) are equivalent to (2.14)–(2.15), respectively. Furthermore, by reasoning similar to (B.11), it follows that

$$S_1(\hat{x}_1,\ldots,\hat{x}_{T-1}) = \frac{1}{1 + \rho^2} \sum_{t=1}^{T-1} \times [(Z_{t+1} - V') - \rho(X_t - V)]^2, \quad \text{(B.19a)}$$

$$S_2(\hat{b}_1,\ldots,\hat{b}_{T-1}) = \frac{1}{1 + \rho^2} \sum_{t=1}^{T-1} [D_{t+1} - \rho B_t]^2. \quad \text{(B.19b)}$$

Substituting (B.19a)–(b) into (B.15a)–(b) gives (2.16)–(2.17).

Finally, if $l(\rho, V')$ is defined by

$$l(\rho, V') = l_2(\rho, V', \hat{x}_1,\ldots,\hat{x}_{T-1}, \hat{b}_1,\ldots,\hat{b}_{T-1}), \quad \text{(B.20)}$$

then (2.18) follows from (B.16) and (B.19). Again, in analogy with (B.13), the proof involves used of the identity

$$(Z_{t+1} - V') - \rho(X_t - V) = (Z_{t+1} - \tilde{Z}) - \rho(X_t - \tilde{X}) + [\tilde{Z} - V' - \rho(\tilde{X} - V)],$$

where $\tilde{X}$ and $\tilde{Z}$ have definitions as for (2.18). This completes the proof of results (2.14)–(2.18) associated with the likelihood function (2.13).

Fish Survival and Recruitment: Investigations Based on a Size-Structured Model

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Schnute, J. T., L. J. Richards, and A. J. Cass. 1989. Fish survival and recruitment: investigations based on a size-structured model. Can. J. Fish. Aquat. Sci. 46: 743–769.

In this paper and its companion (Schnute et al. 1989, Can. J. Fish. Aquat. Sci. 46: 730–742), we present a statistical analysis of Schnute's size-structured model for exploited fish populations. Here we emphasize model parameters associated with survival and recruitment. We present a simple method of graphical analysis for assessing these parameters, and we develop a related statistical model, based on the modern theory of time series analysis. Our model incorporates a range of possible error structures that include both natural variability (process error) and data uncertainty (measurement error). We illustrate the model's application with data from an exploited lingcod (*Ophiodon elongatus*) stock. Preliminary graphical estimates of parameters agree remarkably well with final estimates from the statistical model. Where possible, we investigate alternative viewpoints associated with (1) choices of error structure, (2) dynamic and equilibrium versions of the model, (3) uncertain growth parameters, (4) different abundance indices, (5) mark–recapture experiments, and (6) availability of size-frequency data.

Dans cet article et le précédent (Schnute et coll. 1989, Can. J. Fish. Aquat. Sci. 46: 730–742), nous présentons une analyse statistique du modèle structuré en fonction de la taille de Schnute utilisé pour les populations de poissons exploitées. Dans cet article, nous mettons l'accent sur les paramètres du modèle associés à la survie et au recrutement. Nous présentons une méthode simple d'analyse graphique pour évaluer ces paramètres et nous élaborons un modèle statistique apparenté, basé sur la théorie moderne de l'analyse des séries chronologiques. Notre modèle comprend toute la gamme des erreurs possibles, les erreurs liées à la variabilité naturelle (erreurs liées aux méthodes) et les erreurs liées à l'incertitude des données (erreurs de mesure). Nous illustrons l'application du modèle à l'aide de données provenant d'une population de morue-lingue exploitée (*Ophiodon elongatus*). Les estimations graphiques préliminaires des paramètres concordent remarquablement bien avec les estimations finales réalisées à l'aide du modèle statistique. Dans la mesure du possible, nous étudions d'autres points de vue associés au choix du type d'erreur, aux versions dynamiques et à l'équilibre du modèle, aux paramètres d'incertitude liés à la croissance, à différents indicateurs liés à l'abondance, aux expériences associées au marquage et à la recapture et à la présence de données reliées à la taille et à la fréquence.

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This paper describes a rigorous, practical method of fish stock assessment, using data collected from the fishery. The method applies particularly to cases where annual catch, effort, and size-frequency data are available. Age-frequency data are not required, although the method could readily be applied to such data using "age" as a measure of "size." However, since detailed techniques for assessing catch-at-age data are already available (Fournier and Archibald 1982; Deriso et al. 1985), the method is aimed primarily at stocks for which size (weight or length) data are available but age data are not.

Incentive for this research comes from attempts to apply recent theoretical models for means, variances, and other moments of population size (Deriso 1980; Schnute 1985; Fournier and Doonan 1987; Schnute 1987a). When applied to actual data, these models sometimes give anomalous results, such as an estimate of natural mortality so high that the stock could not survive. If the model is treated as a black box, with fishery data as input and parameter estimates as output, the researcher is left with little recourse in instances of model failure.

In this paper, we build a link between biological models and modern statistical theory. On the biological side, we use Schnute's (1987a) model for a size-structured fish population, although other models could be adapted similarly. We incorporate statistics into the model in two ways. First, we describe simple graphical analyses that give the model significance as a conceptual tool, rather than a mere analytical black box. Second, we connect the dynamic version of the model to time series analysis in a manner suggested by natural assumptions about statistical error in the data. As we explain below, this theoretical development allows us to identify specific reasons for past model failures.

This paper serves as a companion to our earlier paper (Schnute et al. 1989), where we presented statistical counterparts of Schnute's (1987a) deterministic growth equations. Here we extend the statistical analysis to equations for survival and recruitment. We also illustrate the model's application with data from an exploited lingcod (*Ophiodon elongatus*) stock. More precisely, we continue our analysis of this example by using estimates of growth parameters from our earlier paper (Schnute et al. 1989) as input to the present model.

In both papers, our statistical models allow for measurement error in the observed data. Here, we also include process error

TABLE 1. Outline of this paper.

1. Fishery Model Summary
   1A. Model Definitions
   1B. Model Assumptions
   1C. Model Parameters
   1D. Model Conclusions
2. Graphical Analysis
   2A. Analysis with Size-Frequency Data
   2B. Analysis without Size-Frequency Data
3. Model for a Tagged Population
4. Fishery Equilibrium
5. Statistics and Parameter Estimation
   5A. Prototype for a Statistical Model
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7. Illustrative Example: Graphics
   7A. Data Sources
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   7D. Analysis of σ and q
8. Illustrative Example: Statistics
9. Concluding Remarks

Appendix A. Equilibrium Distribution

Appendix B. Exact MA(1) Likelihood

Appendix C. Measurement and Process Error Variances

associated with natural variability in survival and recruitment. General results from time series analysis allow us to develop methods for distinguishing process and measurement error, without reference to data external to the observed series. In our worked example, we show that conclusions depend profoundly on the assumed error structure. In particular, models with pure measurement or pure process error can both give misleading conclusions. For example, least-squares estimates (which essentially correspond to process error) for models such as those of Deriso (1980) or Schnute (1985) can lead to the anomaly mentioned earlier: unrealistically high values of natural mortality.

Where possible, we investigate the data from different viewpoints. First, as described above, we consider several possible error structures. Second, we give both a dynamic and an equilibrium version of the model, and we compare parameter estimates obtained from each. Third, we investigate the effects of uncertainty in growth parameter estimates taken from our companion paper (Schnute et al. 1989). Fourth, since more than one abundance index may be available to describe the dynamics of a population, we consider two such indices in the worked example. Fifth, because the model has a biological basis, we are able to incorporate ancillary data that may be available. Here we accommodate data from a mark–recapture experiment by using a second model whose parameters relate directly to those in the fishery model. Finally, we demonstrate that conclusions from a size-structured model depend on data availability. Schnute (1987a) discusses two possible scenarios, depending on whether or not historical size-frequency data are available. We show that, if pure process or pure measurement error is assumed, the model gives substantially different results for the lingcod example when size-frequency data are ignored. On the other hand, based on the combined error structure proposed here, results without size-frequency data agree favorably with those obtained from the complete data set.

As the discussion so far suggests, this paper covers a range of complex, related topics. Table 1 lists its contents. In section 1, we present the main conclusions of Schnute's (1987a) theory. Our discussion takes advantage of an earlier summary in Schnute et al. (1989), where we focused on using the size distribution to estimate growth parameters. Here, an abundance index (the catch per unit effort, CPUE) provides additional information needed to estimate survival and recruitment parameters. In section 2, we use the model equations to devise a systematic method of data compilation, and we outline an eight-step graphical procedure. This leads to estimates (and even confidence intervals) of model parameters that can be compared with later analytical results. In section 3, we relate the model to data from a mark–recovery experiment and show how to incorporate such data into the graphical analysis in section 2.

In section 4, we obtain an analytic formula for the population size-frequency distribution at equilibrium. We then describe a statistical method for estimating the average annual survival, based on historical sample weight data. In section 5, we present a general statistical model for the dynamic equations of survival and recruitment. The model incorporates concepts from time series analysis associated with a moving average process of order 1 (MA(1)). As discussed above, we show that this statistical formulation represents a compromise between variability in nature (process error) and uncertainty in the actual data (measurement error). Section 6 gives details particular to the models we apply in our worked example.

Sections 7 to 9 are devoted to the example itself. We begin with a graphical analysis (section 7), which we then relate to a rigorous statistical analysis (section 8). We specifically investigate the effects of altering growth parameters, abundance indices, data sources, and error structure. Finally, we discuss the implications of these results for biological interpretation of the fishery (section 9).

Three substantial mathematical developments are required for the analysis here, and we defer the proofs to appendices. Appendix A shows how to obtain the equilibrium distribution discussed in section 4. Appendix B provides a proof of the algorithm for calculating the exact likelihood of an MA(1) process, as described in section 5B. Finally, Appendix C gives details of the approximations required to identify measurement and process errors in the specific models formulated in section 6.

In summary, the broad intent of this paper is to integrate classical descriptions of fish growth, mortality, and recruitment with modern techniques of graphical and time series analysis. Our research has two facets, population dynamics and statistics. The tools developed here take realistic account of the large statistical error in fishery data, and thus make it possible to assess objectively the information content of the data.

1. Fishery Model Summary

In our companion paper (Schnute et al. 1989), we have given a brief summary of Schnute's (1987a) theory for a size-structured fish population. Here we extend that summary to include concepts related to catch, effort, a population index, and mortality due to fishing and natural causes. For simplicity, we adopt a model in which recruitment occurs instantaneously just prior to the fishing year, followed by instantaneous removal of the

catch. This corresponds to the simplest scenario suggested by Schnute (1987a, his equation (3.4)). Although he proposed a variety of alternatives, we find that none of them lead to results substantially different from those presented in the worked example here.

Our description of the model is organized as follows. First (section 1A), we discuss three quantities basic to the model, along with a set of related definitions. We also obtain several simple consequences of these definitions. Second (section 1B), we articulate six assumptions that define our model. Third (section 1C), we discuss the model's parameters and related constraints. Finally (section 1D), we derive a variety of conclusions that follow from the model definitions and assumptions. These govern biomass growth dynamics, biomass indexing, and the partition between fishing and natural mortality. We require a set of conclusions adequate for several contexts, including both graphical and analytical analyses in the cases where size-frequency data are available or not. For easy reference, we assemble the principal results into a table (Table 3).

1A. Model Definitions

The model is constructed from three basic functions of weight w in year t: the population $N(w, t)$, the catch $C(w, t)$, and the abundance index $I(w, t)$. Each of these functions is a density, that is, it must be integrated across a weight interval to give numbers. For example, the integral

$$\int_{w_1}^{w_2} N(w, t)\, dw$$

represents the number of fish in the population at the start of year t that have weights in the interval (w_1, w_2). A similar integral of $I(w, t)$ represents an index of the number of fish in this weight interval at the start of year t, and the corresponding integral of $C(w, t)$ represents the catch in year t of fish with weights in (w_1, w_2).

Schnute's (1987a) model is predicated on two critical weights, a weight V at which a fish becomes fully recruited to the fishery and a weight V' to which a fish grows in 1 yr, having started at weight V. These weights allow the population to be divided into two size groups: newly recruited fish in the weight interval (V, V'), and previously exploited fish in the interval (V', ∞). Fish in the first group have been recruited just prior to the current year, while fish in the second have been recruited earlier and thus have already been exposed to exploitation. The total recruited population consists of these two groups combined, that is, fish in the weight interval (V, ∞).

Table 2 summarizes a variety of population variables that can be defined from $N(w, t)$, $C(w, t)$, and $I(w, t)$ for size-groups associated with the three intervals (V, ∞), (V, V'), and (V', ∞). Some of these have already been defined in Schnute et al. (1989), and most are also defined by Schnute (1987a). For example,

$$(1.1a)\quad N_t = \int_V^\infty N(w, t)\, dw$$

and

$$(1.1b)\quad N_t^* = \int_V^\infty w\, N(w, t)\, dw$$

represent the number of fish and the biomass, respectively, in the total recruited population at the start of year t. Similar integrals of $I(w, t)$ define indices I_t and I_t^* for the abundance and biomass, respectively, of the recruited population at the start of year t. Catch numbers C_t and biomass C_t^* in year t are also defined from integrals of $C(w, t)$ analogous to (1.1).

The integrals (1.1) refer to the weight interval (V, ∞) associated with the total recruited population. Comparable integrals of $N(w, t)$ over (V, V') define the newly recruited population R_t and biomass R_t^*. Similarly, the previously exploited population P_t and biomass P_t^* are defined by integrals of $N(w, t)$ over (V', ∞). Each population and biomass is associated with a related index defined by a corresponding integral of $I(w, t)$. For example, A_t is an index of R_t defined by integrating $I(w, t)$ across the interval (V, V'). As Table 2 shows, indices for R_t, R_t^*, P_t, and P_t^* are labeled A_t, A_t^*, B_t, and B_t^*, respectively.

Quantities defined by integrals can be combined to give definitions of other population variables. For example, the ratios

$$(1.2a)\quad X_t = N_t^*/N_t$$

$$(1.2b)\quad Y_t = R_t^*/R_t$$

$$(1.2c)\quad Z_t = P_t^*/P_t$$

define average weights at the start of year t of fish in the total recruited, newly recruited, and previously exploited components of the population, respectively. Furthermore, abundance and biomass proportions of newly recruited fish at the start of year t are, respectively,

$$(1.3a)\quad \omega_t = R_t/N_t,$$

$$(1.3b)\quad \omega_t^* = R_t^*/N_t^*.$$

The discussion so far shows that all population variables listed in Table 2 are defined by (1.1)–(1.3) or by a simple counterpart

TABLE 2. Summary of notation for population variables in year t, where population components are defined by the three indicated weight intervals. In general, a variable associated with fish biomass is distinguished by a superscript asterisk (*) from the corresponding variable for numbers of fish.

	Population component		
Quantity	Recruited	Newly recruited	Previously exploited
Weight interval	(V, ∞)	(V, V')	(V', ∞)
Population (Numbers)	N_t	R_t	P_t
Population (Biomass)	N_t^*	R_t^*	P_t^*
Mean weight	X_t	Y_t	Z_t
Proportion (Numbers)	1	ω_t	$1-\omega_t$
Proportion (Biomass)	1	ω_t^*	$1-\omega_t^*$
Index (Numbers)	I_t	A_t	B_t
Index (Biomass)	I_t^*	A_t^*	B_t^*
Catch (Numbers)	C_t	$\omega_t C_t$	$(1-\omega_t) C_t$
Catch (Biomass)	C_t^*	$\omega_t^* C_t^*$	$(1-\omega_t^*) C_t^*$

of (1.1). The definitions of these variables imply a number of simple relationships, including

$$(1.4a)\quad N_t = R_t + P_t,$$

$$(1.4b)\quad N_t^* = R_t^* + P_t^*,$$

$$(1.5a)\quad \omega_t = \frac{Z_t - X_t}{Z_t - Y_t},$$

$$(1.5b)\quad \omega_t^* = \frac{Y_t}{X_t} \cdot \frac{Z_t - X_t}{Z_t - Y_t}.$$

Proofs of (1.4)–(1.5) are straightforward. For example, equations (1.4a)–(b) result trivially from the fact that a sum of integrals over (V, V') and (V', ∞) is an integral over (V, ∞). To obtain (1.5a), write (1.4b) in the form

$$X_t N_t = \omega_t Y_t N_t + (1 - \omega_t) Z_t N_t$$

and solve for ω_t. Similarly, (1.5b) follows from (1.4a).

As we show below, one version of our model requires calculating the proportion ω_t^* of newly recruited fish in the total biomass. Notice that (1.5b) gives ω_t^* in terms of the mean weights X_t, Y_t, and Z_t. This is one important way in which size-frequency data enter the calculation.

1B. Model Assumptions

Our summary up to this point consists entirely of definitions related to the basic functions $N(w, t)$, $C(w, t)$, and $I(w, t)$. This structure provides the foundation for stating Schnute's (1987a) model, which (for present purposes) is based on six assumptions. The first is that a fish with weight $w \geq V$ will grow in 1 yr to the weight

$$(1.6)\quad w' = W + \rho w,$$

where W and ρ are constant growth parameters. As explained in our companion paper (Schnute et al. 1989), (1.6) corresponds to the Ford–Walford growth law (Ford 1933; Walford 1946). We again follow Schnute's (1987a) convention that a prime denotes the result of one year's growth. Thus, if u represents a weight, then u' is shorthand for $W + \rho u$. We have already applied this convention in regard to the weight V', required for definitions associated with Table 2.

The second assumption is that, for every weight interval (w_1, w_2) with $w_1 \geq V$,

$$(1.7)\quad \int_{w_1'}^{w_2'} N(w, t+1)\, dw = \tau_t \int_{w_1}^{w_2} N(w, t)\, dw,$$

where τ_t is the fraction of fish that survive from year t to year $t + 1$. This assumption relates annual changes in the population density $N(w, t)$ to the growth of individual fish. For further discussion, see Schnute et al. (1989). It is assumed in (1.7) that survival is not size-selective; thus, τ_t is independent of w.

The third assumption relates overall survival τ_t to natural mortality and catch as follows:

$$(1.8)\quad \tau_t N(w, t) = \sigma[N(w, t) - C(w, t)],$$

where σ is the fraction of fish that survive death from natural causes. In (1.8), σ is presumed independent of both w and t and thus is considered a fixed model parameter. Also, (1.8) assumes that catch is removed from the fishery prior to natural mortality; thus, σ multiplies the difference $N(w, t) - C(w, t)$. Schnute (1987a) suggests alternatives to (1.8) that include, for example, concurrent catch and natural mortality, but we find that these do not alter the principal conclusions in our worked example.

The fourth and fifth assumptions are that the index $I(w, t)$ comes from the ratio of catch $C(w, t)$ to effort E_t,

$$(1.9)\quad I(w, t) = C(w, t)/E_t,$$

and that the index is proportional to the population,

$$(1.10)\quad I(w, t) = qN(w, t).$$

The constant of proportionality q in (1.10) is another model parameter, called the catchability. Notice that (1.9) is the first equation in our discussion to include the effort E_t in year t. Underlying (1.9)–(1.10) is the assumption, consistent with (1.7), that fishing mortality is not size-selective. Thus, $N(w, t)$, $C(w, t)$, and $I(w, t)$ are all proportional as functions of w in a fixed year t.

The sixth and final assumption relates the recruited biomass R_t^* in year t to earlier surviving biomasses:

$$(1.11)\quad R_t^* = \sum_{a=k_1}^{k_2} \pi_a F(\tau_{t-a} N_{t-a}^*),$$

where $F(\cdot)$ is a stock–recruitment function, such as that described by Ricker (1975, p. 282) or Schnute (1987a, p. 928). It is assumed in (1.11) that fish are newly recruited to the fishery between ages k_1 and k_2 and that the model parameters π_a $(a = k_1, \ldots, k_2)$ define the fraction of total recruitment from a single brood year that is newly recruited at age a. An implicit assumption in (1.11) is that the spawning stock consists of the entire recruited biomass in each year. If fish recruit prior to maturity, then (1.11) may need modification, for example, by altering the form of the function $F(\cdot)$.

1C. Model Parameters

If $F(\cdot)$ in (1.11) involves, say, three parameters α, β, and γ, then a complete list of parameters in the model (1.6)–(1.11) is:

$$W, \rho, \sigma, q, \alpha, \beta, \gamma, \pi_{k_1}, \ldots, \pi_{k_2}.$$

Furthermore, the definitions in Table 2 require a knowledge of the two weights V and V'. We assume that V is known from background data on the fishery (as in Schnute et al. 1989), so that the growth law (1.6) determines

$$(1.12)\quad V' = W + \rho V.$$

Furthermore, when $\rho < 1$, Schnute et al. (1989) show that (1.6) implies asymptotic growth with the asymptotic weight $W_\infty = W/(1 - \rho)$. Here we extend the definition of W_∞ to the case $\rho \geq 1$ as follows:

$$(1.13)\quad W_\infty = \begin{cases} W/(1-\rho); & 0 \leq \rho < 1; \\ \infty \quad ; & \rho \geq 1. \end{cases}$$

Thus, W_∞ is a single convenient symbol representing the ultimate size of fish in the population. The density $N(w, t)$ is 0 when $w > W_\infty$.

In our companion paper (Schnute et al. 1989), we have explained that, by (1.12), V' can replace W as a model parameter. Here we assume that estimates and confidence intervals for the growth parameters are available from previous analyses; consequently, our discussion focuses on the remaining parameters. These can be divided into two groups:

$$(1.14)\quad \sigma, q$$

and

(1.15) $\alpha, \beta, \gamma, \pi_{k_1}, \ldots, \pi_{k_2}$,

associated with survival and recruitment, respectively. Some of these parameters are subject to obvious constraints. Natural survival must lie between 0 and 1:

(1.16) $0 \leq \sigma \leq 1$,

and the catchability must be positive:

(1.17) $q > 0$.

Similarly, the recruitment parameters π_a ($a = k_1,\ldots,k_2$) in (1.15) must be proportions,

(1.18) $0 \leq \pi_a \leq 1$,

that sum to 1:

(1.19) $$\sum_{a=k_1}^{k_2} \pi_a = 1.$$

As shown later in our worked example, these constraints can play a useful role in formulating biologically meaningful conclusions from fishery data.

1D. Model Conclusions

To apply the fishery model (1.6)–(1.11), we must derive results that relate specifically to fishery data. Furthermore, if these results are to provide intuitive understanding of the data, they must have clear biological interpretations. We have already proved two key conclusions in Schnute et al. (1989):

(1.20) $N_{t+1} = R_{t+1} + \tau_t N_t$,

(1.21) $N^*_{t+1} = R^*_{t+1} + \tau_t(X'_t/X_t)N^*_t$.

These describe the population in year $t + 1$ as a sum of recruitment in year $t + 1$ and survival from year t, where (1.20) and (1.21) refer to numbers and biomass, respectively. The extra factor X'_t/X_t in (1.21) accounts for fish growth. Furthermore, if R^*_{t+1} in (1.21) is replaced by $\omega^*_{t+1}N^*_{t+1}$ from (1.3b), it follows that

(1.22) $N^*_{t+1} = \upsilon_t\tau_t N^*_t$,

where the factor

(1.23) $$\upsilon_t = \frac{1}{1 - \omega^*_{t+1}} \cdot \frac{X'_t}{X_t}$$

accounts for both growth and recruitment of biomass.

The results (1.20)–(1.22) depend only on the first two model assumptions (1.6)–(1.7). By integrating index assumptions (1.9)–(1.10), it can be shown that

(1.24) $I^*_t = C^*_t/E_t$,

(1.25) $I^*_t = qN^*_t$,

(1.26) $A^*_t = \omega^*_t I^*_t$,

where (1.26) utilizes the definition (1.3b) of ω^*_t. These state that (i) the biomass index I^*_t is the catch biomass per unit effort (CPUE) in year t, (ii) the index I^*_t is proportional to the population biomass N^*_t, and (iii) the CPUE A^*_t on newly recruited fish represents the proportion ω^*_t of total CPUE I^*_t.

If the third model assumption (1.8) is multiplied by q and integrated, it follows that

(1.27) $\tau_t I^*_t = \sigma(I^*_t - qC^*_t)$.

Also, dividing (1.27) by I^*_t and taking account of (1.24) gives

(1.28) $\tau_t = \sigma(1 - qE_t)$.

This represents the total survival τ_t as a product of two factors: (i) survival σ from natural mortality and (ii) survival $1 - qE_t$ from fishing mortality. If q is small (so that $qE_t \ll 1$), then

$$1 - qE_t \simeq e^{-qE_t}.$$

Consequently, (1.28) can be written in the approximate form

(1.29) $\tau_t = e^{-M-qE_t}$,

where $\sigma = e^{-M}$. This expression for total survival can be compared with traditional notation (Ricker 1975, p. 10–11). The instantaneous total mortality rate $M + qE_t$ (Ricker's Z) is the sum of a rate M from natural causes and a rate qE_t (Ricker's F) from fishing.

We have so far obtained three sets of conclusions from the model (1.6)–(1.11): (i) equations (1.20)–(1.22), which describe population dynamics, (ii) equations (1.24)–(1.26), which relate to indexing, and (iii) equations (1.27)–(1.28), which describe the partition between total and natural mortality. We can assemble these results to obtain specific models for the fishery data. Five such models are sufficient for the analysis here, namely:

(1.30a) $I^*_{t+1} = \upsilon_t\tau_t I^*_t$,

(1.30b) $I^*_{t+1} = \sigma\upsilon_t(I^*_t - qC^*_t)$,

(1.31) $$A^*_t = q \sum_{a=k_1}^{k_2} \pi_a F\left(\frac{1}{q}\,\tau_{t-a} I^*_{t-a}\right),$$

(1.32a) $I^*_{t+1} = A^*_{t+1} + \tau_t(X'_t/X_t)I^*_t$,

(1.32b) $I^*_{t+1} = A^*_{t+1} + \sigma(X'_t/X_t)(I^*_t - qC^*_t)$.

Equations (1.30a), (1.31), and (1.32a) follow from (1.22), (1.11), and (1.21), respectively, by including the scale factor q between each population biomass and its corresponding index. Furthermore, (1.30b) and (1.32b) are identical to (1.30a) and (1.32a), respectively, except that τ_t is replaced by (1.28).

Some of the equations obtained here play a role only in the derivations of later equations. In Table 3, we summarize the final results used in the data analyses that follow. For convenience, we refer to these equations in subsequent discussion by their designation in Table 3. Thus, "[1]" and "(1.5b)" indicate the same equation, an expression for calculating ω^*_t. Notice that [1]–[10] are consequences of the definitions in section 1A and the six assumptions developed in section 1B. Thus, they provide a consistent set of equations for examining the data from various viewpoints, all within a single biological framework.

2. Graphical Analysis

To illustrate the conceptual value of the model, we begin by using equations [1]–[10] to formulate a systematic method of graphical analysis. The method necessarily depends on whether or not size-frequency data are available. Here we discuss both possibilities so that, in our worked example, we can assess the significance of size-frequency data to our results.

2A. Analysis with Size–Frequency Data

Suppose that for years $t = 1,\ldots,T$ the following data are available: catch biomass C^*_t, effort E_t, and sample fish weights w_{it} ($i = 1,\ldots,n_t$), where n_t is the number of fish sampled in

TABLE 3. Fishery model equations used in the data analysis here. Each equation is assigned a reference number in square brackets; corresponding numbers from the text are also shown. Except for [2], which defines υ_t, all these results follow from the definitions in section 1A (summarized in Table 2) and the six assumptions (1.6)–(1.11) in section 1B.

[1]	(1.5b)	$\omega_t^* = \frac{Y_t}{X_t} \cdot \frac{Z_t - X_t}{Z_t - Y_t}$
[2]	(1.23)	$\upsilon_t = \frac{1}{1 - \omega_{t+1}^*} \cdot \frac{X_t'}{X_t}$
[3]	(1.24)	$I_t^* = C_t^*/E_t$
[4]	(1.26)	$A_t^* = \omega_t^* I_t^*$
[5]	(1.28)	$\tau_t = \sigma(1 - qE_t)$
[6]	(1.30a)	$I_{t+1}^* = \upsilon_t \tau_t I_t^*$
[7]	(1.30b)	$I_{t+1}^* = \sigma\upsilon_t (I_t^* - qC_t^*)$
[8]	(1.31)	$A_t^* = q \sum_{a=k_1}^{k_2} \pi_a F \left(\frac{1}{q} \tau_{t-a} I_{t-a}^*\right)$
[9]	(1.32a)	$I_{t+1}^* = A_{t+1}^* + \tau_t(X_t'/X_t)I_t^*$
[10]	(1.32b)	$I_{t+1}^* = A_{t+1}^* + \sigma(X_t'/X_t)(I_t^* - qC_t^*)$

year t. Then we recommend the following process of data compilation and preliminary examination:

Step 1

Obtain reasonable estimates for V, V', and ρ by methods such as those described in our companion paper (Schnute et al. 1989). These may come from sources external to the fishery, such as fish sampled in a mark–recapture experiment.

Step 2

Use the historical sample data to find mean weights X_t, Y_t, and Z_t of fish in the intervals (V, ∞), (V, V'), and (V', ∞), respectively. Since X_t and Z_{t+1} are theoretically related by

$$(2.1) \quad Z_{t+1} = V' + \rho(X_t - V)$$

(Schnute et al. 1989, equations (1.14) and (2.1)), one could possibly iterate back to step 1 at this point. The discussion here assumes that analysis of growth parameters (as described by Schnute et al. 1989) is complete and that V, V', and ρ are fixed. To check the consequences of uncertain growth parameters, repeat this entire procedure starting with extreme values of the parameters in step 1.

Step 3

In step 1, V is chosen to be as small as possible, subject to the condition that fishing appears not to be size selective for weights above V. If some fish in the historical samples have weights less than V, it is necessary to adjust the catch C_t^* downward. Thus, if c_t is the sampled proportion of biomass in year t corresponding to fish weighing less than V, then C_t^* should be multiplied by the factor $1 - c_t$. In what follows, C_t^* always refers to this adjusted catch. Conceptually, fish weighing less than V in the catch are treated as part of the natural mortality that precedes recruitment.

Step 4

For $t = 1,\ldots,T$, compute ω_t^*, I_t^*, and A_t^* from [1], [3], and [4], respectively. Incidentally, it might happen that the raw data include catch C_t^* and CPUE I_t^*, rather than catch C_t^* and effort E_t. For example, the CPUE might be measured using a selected sample of landings in the fishery. In this case, the total effective effort E_t would be computed from C_t^* and I_t^* by an obvious variation of [3]:

$$(2.2) \quad E_t = C_t^*/I_t^*.$$

Step 5

For $t = 1,\ldots,T - 1$, compute υ_t from [2] and τ_t from

$$(2.3) \quad \tau_t = I_{t+1}^*/(\upsilon_t I_t^*),$$

where (2.3) is equivalent to [6]. This expression for τ_t represents an empirical estimate of the total survival between years t and $t + 1$. Such an estimate is possible because the size-frequency data enable us to estimate directly the factor υ_t, which accounts for both growth and recruitment.

Step 6

Produce time series plots of the data described in steps 2 to 5: C_t^*, E_t, X_t, Y_t, Z_t, I_t^*, A_t^*, ω_t^*, τ_t, and υ_t. Also, if Q_t represents one of the quantities just listed, then a time series plot of the cumulative sums

$$\sum_{i=1}^{t} Q_i$$

can be used to detect abrupt changes. If Q_t is stable, then the plot of sums looks essentially linear. If Q_t shifts to a different level, then the plot of sums exhibits a change in slope. For further discussion of cumulative sum (CuSum) plots, see Murdoch (1979). In general, both the time series and CuSum plots should be examined for evidence of trends, abrupt changes, and outliers. An abrupt change, for example, may indicate the need for a more complex model to estimate distinct parameters from different time periods.

Step 7

Equation [5] suggests a linear relationship between τ_t and E_t with intercept σ and slope $-\sigma q$. To investigate this possibility, plot τ_t versus E_t. If possible, obtain visual estimates of σ and q. If the constraints (1.16)–(1.17) do not appear satisfied, then the data may be uninformative about these parameters, or the model may be inadequate.

Step 8

To investigate recruitment, as in [8], plot A_t^* versus $\tau_{t-a} I_{t-a}^*$ for various ages a. Obviously, one should select ages that are consistent with available knowledge about recruitment. Each such plot represents [8] when $k_1 = k_2$, that is, when there is a unique age of recruitment. Even if $k_1 \neq k_2$, at least one of these plots (corresponding to the age when π_a is maximum) should exhibit a visible relationship. If not, then the data may simply fail to provide evidence of a stock–recruitment relationship. In this case, an overall constant level of recruitment

$$(2.4a) \quad A_t^* = A^*,$$

where A^* is a positive parameter,

$$(2.4b) \quad A^* > 0,$$

may be all the information available from the data. This does not, of course, mean that recruitment actually is constant; rather, the noise level in the data masks any stock–recruitment relationship that exists.

The analysis described in steps 1 to 8 can be implemented with modern "spreadsheet" software, oriented to rows and columns of numbers. Such software makes it easy, first, to perform

the calculations indicated in steps 4 and 5 by creating new data columns from existing columns and, second, to produce the graphs suggested in steps 6 to 8. Obviously, it would be a sizeable task to prepare all these graphs by hand, and our suggestions for graphical analysis are predicated on access to modern computing technology.

2B. Analysis without Size–Frequency Data

If historical sample weights are not available, then data for the model are limited to two time series, catch biomass C_t^* and effort E_t for $t = 1,\ldots,T$. For these restricted data, the analysis above needs significant modification, because the processes of survival and recruitment are confounded. In an attempt to distinguish these processes, we focus here on two special cases of [9]:

$$(2.5)\quad I_{t+1}^* = A^* + \tau_t(X'/X)I_t^*,$$

$$(2.6)\quad I_{t+1}^* = A_{t+1}^* + \tau(X'/X)I_t^*,$$

where the mean weight X is presumed independent of t. These equations contemplate two extremes for the model dynamics. In (2.5) recruitment is constant, and A^* is an associated recruitment parameter; variability is explained by the survival factor τ_t. By contrast, (2.6) assumes constant survival τ (a parameter) and variable recruitment A_{t+1}^*. We recommend the following preliminary analysis based on (2.5)–(2.6):

Step 1

From sources external to the data, obtain an estimate for the average fish weight X and the weight X' to which a fish of weight X would grow in 1 yr. This may, for example, involve independent estimates of the model's growth parameters.

Step 2

For $t = 1,\ldots,T$, use [3] to calculate I_t^* from C_t^* and E_t. As in section 2A (step 4), it may alternatively be appropriate to use (2.2) to calculate E_t.

Step 3

Let $\bar{I}^*$ represent a typical value of I_t^*, such as the mean or geometric mean. Plot A^* as a function of τ from the following equilibrium version of (2.5)–(2.6):

$$(2.7)\quad A^* = \bar{I}^* - \tau(X'/X)\bar{I}^*.$$

This linear function expresses the average trade-off between recruitment and survival. For example, as the survival τ decreases, the corresponding recruitment index A^* must increase to be consistent with $\bar{I}^*$.

Step 4

Plot I_{t+1}^* versus $(X'/X)I_t^*$, and inspect the resulting scatter plot for a linear relationship

$$(2.8)\quad I_{t+1}^* = A^* + \tau(X'/X)I_t^*.$$

Determine visually a low, reasonable, and high estimate for the intercept A^*. Then find a corresponding high, reasonable, and low estimate for the slope τ, respectively, with reference to the linear relationship (2.7) between A^* and τ.

Step 5

For $t = 1,\ldots,T-1$, compute three time series

$$(2.9)\quad \tau_t = \frac{I_{t+1}^* - A^*}{(X'/X)I_t^*}$$

from the three estimates A^* obtained in step 4. Similarly, for $t = 2,\ldots,T$, compute three time series

$$(2.10)\quad A_t^* = I_t^* - \tau(X'/X)I_{t-1}^*$$

from the three estimates τ obtained in step 4. Notice that formulas (2.9)–(2.10) are based on models (2.5)–(2.6), respectively. Thus, the series τ_t represents an empirical measure of survival from year t to $t+1$, based on a constant recruitment index A^*. Similarly, A_t^* represents an empirical recruitment index in year t, given the constant survival τ.

Step 6

As in section 2A (step 6) produce time series and CuSum plots of the following data: C_t^*, E_t, I_t^*, τ_t, and A_t^*. From step 5, these include three plots of τ_t and A_t^*. As before, investigate all plots for trends, abrupt changes, and outliers.

Step 7

For each series τ_t from step 5, examine a scatter plot of τ_t versus E_t for evidence of the linear relationship [5]. As in section 2A (step 7), obtain visual estimates of σ and q for each case, if possible.

Step 8

As in section 2A (step 8), plot A_t^* versus τI_{t-a}^* for various ages a. Three such plots are possible from steps 4 and 5, based on three estimates for τ and three corresponding series A_t^*. Investigate these graphs for evidence of a stock–recruitment relationship.

The general philosophy underlying steps 1 to 8 above is to mimic, as far as possible, the analysis with size-frequency data. One can compensate for the absence of these data by assuming that either survival or recruitment is constant. In the case of constant survival, for example, one can use empirical estimates of recruitment to assess the validity of a stock–recruitment relationship. Similarly, if recruitment is constant, then empirical survival estimates can be used to assess the impact of fishing effort on total mortality. By considering several values of the fixed parameter (survival or recruitment), it is possible to gauge the model's ability to detect various relationships. In the worked example below, we show explicitly how size-frequency data supply information that improves the model's ability to discern both recruitment and survival parameters.

3. Model for a Tagged Population

In our companion paper (Schnute et al. 1989), we described how weights of fish from a mark–recovery experiment could be used as supplementary data for the model's growth parameters. Similarly, the numbers of fish released and recovered can provide information on survival and catchability. To be specific, consider the following experiment. In the first year ($t = 1$), N_1 fish are tagged and returned to the sea. Later that same year, C_1 of these fish are caught with an associated effort E_1. In subsequent years ($t = 2,\ldots,T$), the number of fish caught and the related effort are C_t and E_t, respectively. Data from this experiment, then, are comparable with the fishery data discussed in section 2. Both circumstances involve a time series of catch and effort data.

There are three key differences, however, between the group of tagged fish and the population in the fishery. First, for the tagged group, an initial population N_1 is known; in the fishery, the population can never be measured directly. Second, catch is measured in numbers for the tagged group, while catch bio-

mass is recorded in the fishery. Third, unlike the population in the fishery, the tagged group experiences no recruitment. Each of these differences makes the model for the tagged population simpler than that for the fishery.

To build a tagged population model, let N_t represent the remaining number of tagged fish at the start of year t. Each of the six assumptions (1.6)–(1.11) in the fishery model either leads to a corresponding assumption for the tagged group or is inapplicable. It turns out that (1.6) and (1.11) do not apply here, because the growth of tagged fish is ignored and there is no recruitment. Assumptions corresponding to (1.7)–(1.10) are, respectively,

$$(3.1)\quad N_{t+1} = \tau_t N_t,$$

$$(3.2)\quad \tau_t N_t = \sigma(N_t - C_t),$$

$$(3.3)\quad I_t = C_t/E_t,$$

$$(3.4)\quad I_t = qN_t.$$

Thus, the model assumes that I_t, the catch (in numbers) per unit effort, indexes the remaining tagged population N_t.

The fishery model (1.6)–(1.11) and the tagged population model (3.1)–(3.4) have identical biological foundations. If the tagged fish truly represent the stock from which they come, then values of σ and q should agree between the two models. Furthermore, the tag model (3.1)–(3.4) implies that

$$(3.5)\quad I_1 = qN_1,$$

$$(3.6)\quad I_{t+1} = \sigma(I_t - qC_t),$$

for $t = 1,\ldots,T-1$. These equations suggest that the tag data should be adequate for estimating q and σ. For example, from (3.5) an estimate for q is N_1/I_1. Similarly, if q is known, then from (3.6) an estimate for σ is a typical value of the ratio $I_{t+1}/(I_t - qC_t)$. By contrast, the fishery data do not include a known population, such as N_1 here. Consequently, those data provide no direct estimate of q, such as that from (3.5). Although indirect estimates of q are possible from fishery data, it appears that the tag data may provide valuable supplementary information. Another possibility, however, is that tagged fish may experience natural and fishing mortalities that are not characteristic of the general population. In this case, the parameters q and σ in (3.5)–(3.6) may differ from their counterparts in the fishery model.

To assess the relationship between tag and fishery data, it is possible to include tag data in graphical analysis of section 2. Here we consider only the case (section 2A) when size-frequency data are available from the fishery. In step 5, use tag data to compute an independent estimate of τ_t from the following counterpart of (2.3):

$$(3.7)\quad \tau_t = I_{t+1}/I_t,$$

where (3.7) follows from assumption (3.1). Next, in step 6, include both fishery and tag estimates in the time series plot of τ_t. In step 7, one can compare the scatter plot of τ_t versus E_t from the fishery with that from tag data. In both cases, [5] should theoretically apply. Step 8, of course, does not apply to the tagged group, since no recruitment is involved.

Typically, the number of years T of fishery data is much larger than the number of years for which tag data are available. Consequently, as in the worked example later, the tag data may provide relatively few data points for the analysis. Nevertheless, tag and fishery data can be compared in graphs related to survival, just as they were compared in graphs related to growth in our companion paper (Schnute et al. 1989). In both papers, then, we relate a feature of the entire population to a similar feature in a small group of individuals.

4. Fishery Equilibrium

The fishery model (1.6)–(1.11) is dynamic, that is, it describes changes in the population from one year to the next. Although this feature of the model mirrors the dynamic character of the fishery, an equilibrium version may also have considerable practical significance. Intuitively, when the population is at equilibrium, the effects of growth, survival, and recruitment are balanced. Furthermore, recruitment is constant and acts primarily as a scale factor. The population's size structure, then, is determined by the balance between growth and survival. For example, if fish are known to grow slowly and if numerous large fish are present in population, then survival must be high to account for the presence of these large fish. In general, survival parameters are linked with growth parameters at equilibrium, and mean size structure can be used to make inferences about one set of parameters from the other. In this section we derive the equilibrium distribution that makes such inferences possible.

The model's dynamics are contained primarily in assumption (1.7). If $N(w, t)$ and τ_t do not depend on t, then (1.7) becomes

$$(4.1)\quad \int_{w_1'}^{w_2'} N(w)\,dw = \tau \int_{w_1}^{w_2} N(w)\,dw.$$

This equation is valid for every interval (w_1, w_2) with $w_1 \geq V$. For integer values of t, it describes the transition from time t to $t+1$. Our analysis of equilibrium requires a minor alteration of (4.1) to continuous time. This change is consistent both with the assumptions made so far and with the concept of equilibrium, in which growth and mortality occur continuously. In Appendix A, we convert (4.1) to continuous time and derive the equilibrium distribution

$$(4.2)\quad N(w) = N_v \left[\frac{(V' - w) - \rho(V - w)}{V' - V}\right]^{\log(\tau/\rho)/\log(\rho)},$$

where the constant N_v is the density of fish with weight V. This result applies to weights w in the interval (V', W_∞), with $N(w) = 0$ for $w > W_\infty$. (See (1.13).) Thus, the continuous-time counterpart of (4.1) determines $N(w)$ completely, except for the constant N_v.

By integrating (4.2) from V to W_∞, it is possible (Appendix A) to compute the total population

$$(4.3)\quad N = N_v \cdot \frac{V' - V}{1 - \rho} \cdot \frac{\log(\rho)}{\log(\tau)}.$$

Furthermore, the probability density $\theta(w)$ for fish of weight w within the population is the ratio

$$\theta(w) = N(w)/N.$$

Thus, from (4.2)–(4.3), $\theta(w)$ is given by

$$(4.4)\quad \theta(w) = \frac{1 - \rho}{V' - V} \cdot \frac{\log(\tau)}{\log(\rho)} \cdot \left[\frac{(V' - w) - \rho(V - w)}{V' - V}\right]^{\log(\tau/\rho)/\log(\rho)}$$

The constant N_V cancels when computing this ratio. Consequently, the equilibrium probability distribution $\theta(w)$ is determined by the parameters V, V', ρ, and τ.

The cumulative distribution

$$\Theta(w) = \int_V^w \theta(u)\, du$$

can also be computed analytically. It turns out (Appendix A) to be given by

$$(4.5)\quad \Theta(w) = 1 - \left[\frac{(V' - w) - \rho(V - w)}{V' - V}\right]^{\log(\tau)/\log(\rho)},$$

a formula somewhat simpler than (4.4). Notice, in particular, that $\Theta(w)$ varies from 0 to 1:

$$(4.6a)\quad \Theta(V) = 0,$$

$$(4.6b)\quad \Theta(W_\infty) = 1.$$

When $\rho < 1$, (4.6b) is a consequence of the following property of W_∞:

$$W_\infty - V' = \rho(W_\infty - V);$$

when $\rho \geq 1$ (and $W_\infty = \infty$), (4.6b) expresses the fact that

$$\lim_{w \to \infty} \Theta(w) = 1.$$

Incidentally, equations (4.4)–(4.5) are not defined when $\rho = 1$, due to division by $\log(\rho)$. Nevertheless, both $\theta(w)$ and $\Theta(w)$ have limits (Appendix A) as ρ tends to 1:

$$(4.7)\quad \theta(w) = -\frac{\log(\tau)}{V' - V} \cdot \tau^{(w-V)/(V'-V)},$$

$$(4.8)\quad \Theta(w) = 1 - \tau^{(w-V)/(V'-V)}.$$

To understand the biological significance of (4.4)–(4.5), it is helpful to compute $\theta(w')$ and $\Theta(w')$, where, as usual, w' denotes the result of one year's growth from w. These calculations (Appendix A) lead to the following simple properties of θ and Θ:

$$(4.9)\quad \theta(w') = (\tau/\rho)\theta(w),$$

$$(4.10)\quad 1 - \Theta(w') = \tau[1 - \Theta(w)].$$

Since $1 - \Theta$ represents the tail of the distribution Θ, (4.10) states that the tail corresponding to w' represents the fraction τ of the tail corresponding to w. This is exactly what one might expect from the combined effects of growth and survival. The w'-tail represents fish 1 yr older than those represented by the w-tail. The older fish have experienced an extra year's mortality, so that their probability in the population is reduced by the factor τ. The significance of (4.9) is similar, except that the extra factor $1/\rho$ accounts for the fact that $\theta(w)$ is a probability density, rather than a probability. Incidentally, the properties (4.9)–(4.10) are particularly easy to prove from (4.7)–(4.8) when $\rho = 1$. In this case, $w' = w + V' - V$.

The results (4.4)–(4.5) differ in two keys ways from all previous results in this paper. First, they describe the entire weight distribution, not just the compiled mean weights (X_t, Y_t, Z_t). Second, they apply specifically to a stable fishery. Notice from [5] that, if the fishery is stable with essentially constant effort E, then natural and fishing mortalities are confounded in the single parameter τ:

$$(4.11)\quad \tau = \sigma(1 - qE).$$

The explicit formulas (4.4)–(4.5) suggest that this overall survival τ could be estimated from observed size-frequency data.

One possible estimate can be obtained as follows. Assume, as usual, that the parameters V, V', and ρ are known. Let $\hat{\Theta}(w)$ represent the annual weight distribution, averaged over the historical period, and let $\Theta(w; \tau)$ be the theoretical distribution (4.5). Then the function

$$(4.12)\quad \kappa(\tau) = \max_w |\Theta(w; \tau) - \hat{\Theta}(w)|$$

is the Kolmogorov statistic (Kendall and Stuart 1979, p. 477) associated with the difference between these two distributions. The minimum of $\kappa(\tau)$ provides an estimate $\hat{\tau}$ of τ. Our worked example illustrates this procedure.

5. Statistics and Parameter Estimation

Except for the definition (4.12) above, our discussion so far has avoided the statistical link between model equations and actual data. We have either treated the model deterministically or proposed graphs that indicate the model–data relationship visually. To derive analytical methods for estimating parameters and confidence intervals, we need to specify statistical counterparts of various model equations. Unfortunately, it is not immediately obvious how to include statistical error in the time series models obtained earlier. Furthermore, as we show in our worked example, the choice of error structure can have an important effect on the resulting parameter estimates.

We recognize, of course, that time series analysis has been the subject of intense study (Box and Jenkins 1970) and that certain general methods have met with success in a variety of fields. Our strategy is to apply these methods by linking them with the biologically based models here. We illustrate the basic concept with a simple prototype (section 5A) and then present a more general framework (section 5B), where we derive an exact formula for the likelihood function. We also describe methods of assessing confidence in the parameter estimates (section 5C) obtained by maximum likelihood.

5A. Prototype for a Statistical Model

Consider, for example, the case in which available data include the time series I_t^*, C_t^*, and υ_t for $t = 1,\ldots,T$ as in section 2A. For simplicity in our prototype, assume that the series υ_t is essentially constant, $\upsilon_t = \upsilon$. The survival model [7] then takes the form

$$I_t^* = \sigma\upsilon(I_{t-1}^* - qC_{t-1}^*),$$

where t is replaced by $t - 1$ for convenience in the calculations below. A simple statistical counterpart of this model is

$$(5.1)\quad I_t^* = \sigma\upsilon(I_{t-1}^* - qC_{t-1}^*) + \phi\epsilon_t,$$

where (i) ϕ represents the standard deviation of error and (ii) the random variables ϵ_t are assumed to be independent and normal with mean 0 and variance 1. The likelihood function for $\epsilon_2,\ldots,\epsilon_T$ is the following product of normal probability densities:

$$(5.2)\quad L = (\sqrt{2\pi}\,\phi)^{-(T-1)} \exp\left[-\frac{1}{2\phi^2}\sum_{t=2}^{T}\epsilon_t^2\right].$$

Thus, it appears that the likelihood associated with (5.1) should be

$$(5.3)\quad L = (\sqrt{2\pi}\,\phi)^{-T+1} \cdot \exp\left[-\frac{1}{2\phi^2}\sum_{t=2}^{T}(I_t^* - \sigma\upsilon I_{t-1}^* + \sigma q\upsilon C_{t-1}^*)^2\right].$$

This is almost correct if it is assumed that the data υ and C_t^* are not subject to statistical error. Even then, (5.3) needs slight modification to account for statistical properties of the initial observation I_1^*. (For further discussion of this point in a slightly different context, see Schnute 1987b, p. 204–208). Usually, this correction is small and can be safely ignored. If the distribution of I_1^* is independent of model parameters, then (5.3) defines the exact likelihood function $L(\sigma, q, \phi)$ for (5.1).

Parameter estimates can be obtained from (5.3) by maximizing $L(\sigma, q, \phi)$. In particular, if σ and q are specified, then the corresponding estimate for ϕ turns out to be

$$(5.4)\quad \hat{\phi}^2 = \frac{1}{T-1}\sum_{t=2}^{T}(I_t^* - \sigma\upsilon I_{t-1}^* + \sigma q\upsilon C_{t-1}^*)^2.$$

To obtain estimates for σ and q, define

$$(5.5)\quad l(\sigma, q) = -2\cdot\log[L(\sigma, q, \hat{\phi})] - (T-1)\cdot \log[2\pi e/(T-1)],$$

where e is the base for natural logarithms. Thus, l is twice the negative log likelihood, except for a constant, evaluated at $\hat{\phi}$. It turns out that

$$(5.6)\quad l(\sigma, q) = (T-1)\cdot \log\left[\sum_{t=2}^{T}(I_t^* - \sigma\upsilon I_{t-1}^* + \sigma q\upsilon C_{t-1}^*)^2\right].$$

By (5.5), maximum likelihood estimates $\hat{\sigma}$ and $\hat{q}$ correspond to the minimum of $l(\sigma, q)$. In particular, these estimates can be obtained by minimizing the sum of squares in (5.6). Furthermore, based on the likelihood ratio test (Kendall and Stuart 1979, chapter 24), the boundary of an approximate $100\cdot p\%$ confidence region for the parameter pair (σ, q) is defined by

$$(5.7)\quad l(\sigma, q) = l(\hat{\sigma}, \hat{q}) + \chi^2(2, p),$$

where $\chi^2(2, p)$ represents the cutoff at level p $(0 < p < 1)$ for the χ^2-distribution with 2 *df*.

From a practical point of view, the above argument seems very attractive. The function $l(\sigma, q)$ in (5.6) provides a technical device for using fishery data both to estimate the survival parameters (σ, q) and to obtain a confidence region for them. Unfortunately, the model (5.1) is inadequate for most fishery data. Typically, the catch and size-frequency data are relatively well known, but the effort (or, equivalently, CPUE) data are poorly known. This much is consistent with our assumption that the likelihood function relates to the data I_t^*, not C_t^*, or υ. However, the model (5.1) treats I_{t-1}^* as a known value in the prediction of I_t^*. In reality, both I_{t-1}^* and I_t^* often involve significant measurement error.

A revision of (5.1) that accounts for this problem is

$$(5.8a)\quad J_t^* = \sigma\upsilon(J_{t-1}^* - qC_{t-1}^*) + \phi\epsilon_t,$$

$$(5.8b)\quad I_t^* = J_t^* + \psi\delta_t,$$

where (i) J_t^* is an unknown true value of the CPUE in year t, (ii) ϕ and ψ are standard deviations of error, and (iii) ϵ_t and δ_t are independent random variables with mean 0 and variance 1. Biologically, J_t^* represents an index that is exactly proportional to N_t^*, and I_t^* is an erroneous measurement of J_t^*. Equation (5.8a) relates to the dynamic behavior of N_t^*, which also involves statistical error in the transition from one year to the next. Thus, model (5.8) includes both measurement error $(\psi\delta_t)$ and process error $(\phi\epsilon_t)$, where the error variances are ψ^2 and ϕ^2, respectively.

When $\psi = 0$, (5.8) is identical to (5.1), a model with pure process error. By contrast, when $\phi = 0$, (5.8) defines a pure measurement error model, in which the time series J_t^* is calculated deterministically from (5.8a). If J_1^* is considered an unknown parameter and if $J_t^*(\sigma, q, J_1^*)$, $t = 2,\ldots,T$, is calculated iteratively from (5.8a) with $\phi = 0$, then the counterpart of (5.6) for this case is

$$(5.9)\quad l(\sigma, q, J_1^*) = (T-1)\cdot\log\left(\sum_{t=2}^{T}[I_t^* - J_t^*(\sigma, q, J_1^*)]^2\right).$$

In contexts similar to the one here, researchers (e.g. Jacobson et al. 1987) have tried using likelihood functions similar to both (5.6) and (5.9). Schnute (1987b, section 2) gives a simple argument showing why the least squares estimate of slope can be small, and an application of his argument suggests that (5.6) might lead to an underestimate of $\sigma\upsilon$ (the slope in the relationship between I_{t-1}^* and I_t^*). Indeed, researchers often obtain such a low estimate of survival, and resort to (5.9) as an alternative.

Unfortunately, both assumptions $\psi = 0$ and $\phi = 0$ appear unreasonable. They represent extremes, respectively, in which either (i) the CPUE perfectly indexes the population biomass or (ii) natural processes introduce no variability in the transition from one year to the next. Since model (5.8) offers a compromise between these extremes, we evidently need to derive a likelihood function for (5.8) that generalizes (5.6) and (5.9). To do this, eliminate J_t^* from (5.8a)–(b) to obtain

$$(5.10a)\quad I_t^* = \sigma\upsilon(I_{t-1}^* - qC_{t-1}^*) + \eta_t,$$

where

$$(5.10b)\quad \eta_t = \phi\epsilon_t + \psi(\delta_t - \sigma\upsilon\delta_{t-1}).$$

This is similar to (5.1), except that the residuals η_t have a more complex statistical structure. The residuals in (5.1) have constant variance ϕ^2 and are uncorrelated; by contrast,

$$(5.11a)\quad \mathrm{Var}[\eta_t] = \phi^2 + \psi^2(1 + \sigma^2\upsilon^2),$$

$$(5.11b)\quad \mathrm{Cov}[\eta_t, \eta_{t-1}] = -\psi^2\sigma\upsilon.$$

Technically, the residual covariance matrix for (5.1) is diagonal, with the value ϕ^2 along the main diagonal. The analogous matrix for (5.10) is tri-diagonal; it involves both variance parameters ϕ^2 and ψ^2, as well as the survival parameter σ.

The model (5.10) can be converted to a form consistent with modern time series analysis by writing it as follows:

$$(5.12a)\quad I_t^* = \sigma\upsilon(I_{t-1}^* - qC_{t-1}^*) + \eta_t,$$

$$(5.12b)\quad \eta_t = \xi(\epsilon_t - \lambda\epsilon_{t-1}).$$

Here, as before, the variates ϵ_t are independent and normal with mean 0 and variance 1. Also the residuals η_t have a tri-diagonal covariance matrix determined by the parameters ξ and λ:

$$(5.13a)\quad \mathrm{Var}[\eta_t] = \xi^2(1 + \lambda^2),$$

$$(5.13b)\quad \mathrm{Cov}[\eta_t, \eta_{t-1}] = -\xi^2\lambda.$$

In the language of time series analysis (Box and Jenkins 1970), the residuals η_t in (5.12) result from a moving average process of order 1, commonly denoted MA(1). For theoretical reasons (Box and Jenkins 1970, p. 284, Appendix A7.6), the parameters ξ and λ must be constrained:

$$(5.14)\quad \xi > 0,\ -1 \leq \lambda \leq 1.$$

It follows that models (5.10) and (5.12) are identical if the covariance matrices agree:

$$\phi^2 + \psi^2(1 + \sigma^2\upsilon^2) = \xi^2(1 + \lambda^2), \tag{5.15a}$$

$$\psi^2\sigma\upsilon = \xi^2\lambda. \tag{5.15b}$$

Thus, these models differ only in the choice of variance parameters , (ϕ, ψ) or (ξ, λ), and equations (5.15) allow one pair to be converted to the other. For example, if (ξ, λ) is known, then

$$\phi^2 = \xi^2(\lambda - \sigma\upsilon)\left(\lambda - \frac{1}{\sigma\upsilon}\right), \tag{5.16a}$$

$$\psi^2 = \frac{\xi^2\lambda}{\sigma\upsilon}. \tag{5.16b}$$

There are, however, legitimate pairs (ξ, λ) without a corresponding (ϕ, ψ). For instance, if λ is negative, then ψ is not defined in (5.16b).

From (5.16), it follows that (5.12) includes both measurement and process error models as special cases. Thus, when $\lambda = 0$, (5.16b) shows that $\psi = 0$; that is, the model is based entirely on process error. This is also evident by direct comparison between (5.1) and (5.12) with $\lambda = 0$. Furthermore, it follows from (5.16a) that $\phi = 0$ if $\lambda = \sigma\upsilon$ or $\lambda = 1/(\sigma\upsilon)$. Since these two values are reciprocals of each other, one of them must have magnitude less than or equal to 1, as required by (5.14). Consequently, (5.12) corresponds to a pure measurement error model when

$$\lambda = \min\left[\sigma\upsilon, \frac{1}{\sigma\upsilon}\right]. \tag{5.17}$$

Our prototype illustrates a general principle for dynamic biological models that involve one time step with combined process and measurement error. Such models can be linked to modern time series analysis simply by adding an MA(1) residual term. We next derive the likelihood function for this class of generalized MA(1) models. Later (section 6) we show how to apply this likelihood to models more realistic (and complex) than the prototype above.

5B. Likelihood for MA(1) Models

To allow flexibility in model development, we describe the required likelihood using generalized notation. Let Q_t, $t = 1,\ldots,T$, represent an observed time series associated with the model

$$Q_t = H(Q_{t-1},\ldots,Q_{t-K};\Phi) + \eta_t, \tag{5.18a}$$

$$\eta_t = \xi(\epsilon_t - \lambda\epsilon_{t-1}), \tag{5.18b}$$

for $t = K + 1,\ldots,T$, where the function $H(\cdot)$ depends on a parameter vector Φ and values of Q_t, back to lag K. As before, ξ and λ are parameters related to the covariance matrix (5.13) of η_t, and the independent variates ϵ_t are normal with mean 0 and variance 1. Notice that (5.12) is a special case of (5.18) with $Q_t = I_t^*$, $K = 1$, $\Phi = (\sigma, q)$, and

$$H = \sigma\upsilon(Q_{t-1} - qC_{t-1}^*),$$

where υ and C_t^* are considered data known without statistical error. Another possibility for (5.18) is a model similar to (5.12) in which I_t^* is transformed by, say, the square root. Such a model can be obtained by defining $Q_t = (I_t^*)^{1/2}$, $K = 1$, $\Phi = (\sigma, q)$, and

$$H = [\sigma\upsilon(Q_{t-1}^2 - qC_{t-1}^*)]^{1/2}.$$

In the worked example below, we use this transform to produce homoscedastic variance in the model residuals. In general, (5.18) can provide a statistical counterpart to any of the models discussed in section 2, including recruitment models that involve a lag $K > 1$. (Incidentally, it might be argued that such models should have MA(K) residuals with $K > 1$, but we do not explore this point further here.)

It remains to define the likelihood function for (5.18). As in (5.6) and (5.9), one might expect that this function would involve a sum S of squared residuals. For example, given Φ, $\eta_t(\Phi)$ could be calculated from (5.18a), and $S(\Phi)$ could be defined as the sum of $\eta_t^2(\Phi)$. Unfortunately, this simplistic procedure is essentially the same as that in (5.6), and it is wrong because it fails to account for correlations among the residuals η_t. A better approach would be to define $\epsilon_t(\Phi)$ iteratively from $\eta_t(\Phi)$ by (5.18b), and then to let $S(\Phi)$ be the sum of $\epsilon_t^2(\Phi)$. The trouble with this method is that it requires an unknown value ϵ_K to start the iterative process. Schnute (1985, p. 426) suggested in a similar context that ϵ_K be treated as an extra model parameter. This is a poor suggestion for several technical reasons, most notably that a simple calculation of the exact likelihood is possible.

We now give a detailed algorithm for calculating this exact likelihood. The algorithm involves a stepwise procedure that leads ultimately to the function $l(\Phi, \lambda)$ in (5.25) below. In analogy with the derivation of (5.6), we assume that the first K observations $Q_1,\ldots,Q_K$ in (5.18) are independent of model parameters. As proved in Appendix B, the exact likelihood function for (5.18) can be calculated by the following steps, starting with given values of Φ and λ:

Step 1

For $t = K + 1,\ldots,T$, compute the model residuals at Φ,

$$\eta_t(\Phi) = Q_t - H(Q_{t-1},\ldots,Q_{t-K};\Phi). \tag{5.19}$$

Step 2

Use λ to determine the value of

$$D(\lambda) = \begin{cases} [1 - \lambda^{2(T-K+1)}]/[1 - \lambda^2] & \text{if } |\lambda| \neq 1, \\ T - K + 1 & \text{if } |\lambda| = 1. \end{cases} \tag{5.20}$$

Step 3

For $t = K + 1,\ldots,T$, calculate the exponentially weighted residuals

$$\zeta_t(\Phi, \lambda) = \sum_{s=1}^{t-K} \lambda^{t-K-s}\eta_{s+K}(\Phi). \tag{5.21}$$

The sums (5.21) can be evaluated efficiently by the iterative formula:

$$\zeta_t(\Phi, \lambda) = \eta_t(\Phi) + \lambda\zeta_{t-1}(\Phi, \lambda), \tag{5.22}$$

starting with $\zeta_K = 0$.

Step 4

Calculate

$$\delta_K(\Phi, \lambda) = -\frac{1}{D(\lambda)} \sum_{t=1}^{T-K} \lambda^t\zeta_{t+K}(\Phi, \lambda), \tag{5.23a}$$

and, for $t = K + 1,\ldots,T$,

$$\delta_t(\Phi, \lambda) = \zeta_t(\Phi, \lambda) + \lambda^{t-K}\delta_K(\Phi, \lambda). \tag{5.23b}$$

Step 5

Compute the sum of squares

$$(5.24)\quad S(\Phi, \lambda) = \sum_{t=K}^{T} \delta_t^2(\Phi, \lambda).$$

Step 6
Finally, calculate

$$(5.25)\quad l(\Phi, \lambda) = \log[D(\lambda)] + (T - K) \cdot \log[S(\Phi, \lambda)].$$

This function is twice the negative log likelihood (except for a constant) for model (5.18), evaluated at the maximum likelihood estimate $\hat{\xi}$ of ξ. Furthermore, as shown in Appendix B,

$$(5.26)\quad \hat{\xi}^2(\Phi, \lambda) = S(\Phi, \lambda)/(T - K).$$

To understand the definition of l intuitively, notice first that η_t in (5.19) corresponds exactly to the model residual in (5.18a). The iterative rule (5.22) for ζ_t matches (5.18b), if ζ_t is identified with $\xi\epsilon_t$. Thus, the series ζ_t can be considered a first estimate of the uncorrelated residuals $\xi\epsilon_t$, starting with $\epsilon_K = 0$. The formula (5.23a) for δ_K is a revised estimate of $\xi\epsilon_K$, in fact, a maximum likelihood estimate. Based on this revised estimate, (5.23b) defines revisions δ_t for the remaining uncorrelated residuals $\xi\epsilon_t$. The sum S of these residuals squared is then used to define the likelihood l and the estimate $\hat{\xi}^2$. Finally, the quantity $D(\lambda)$ represents the determinant of the covariance matrix (5.13) for η_t, divided by ξ^2. This determinant enters the calculation as part of the multivariate normal probability distribution for the residuals η_t.

If $\lambda = 0$ in the above calculation, notice that $D = 1$, $\delta_K = 0$, and, for $t = K + 1,\ldots,T$:

$$\eta_t = \zeta_t = \delta_t.$$

Thus the uncorrelated residuals δ_t are simply the model residuals η_t, and the maximum likelihood estimate for Φ corresponds to the usual least squares estimate. In particular, (5.6) is a special case of (5.25) when $\lambda = 0$. More generally, when $\lambda \neq 0$, the estimation problem is still related to least squares, except that the uncorrelated residuals δ_t are essentially exponentially weighted sums of the model residuals η_t. We examine the significance of the extra parameter λ in the worked example below.

5C. Profiles and Confidence Regions

Having defined the likelihood for model (5.18), we can now describe its use in estimating parameters and confidence regions. To simplify the discussion, let

$$\Psi = (\Phi, \lambda)$$

denote the full vector of model parameters, except for ξ. Then Ψ can be estimated by minimizing $l(\Psi)$ in (5.25), and a corresponding estimate for ξ is given by (5.26). Furthermore, $l(\Psi)$ can be used in a manner analogous to (5.7) to determine a confidence interval for any single parameter or a confidence region for any parameter pair.

For example, let ψ_1 denote any single parameter in the vector Ψ, and let Ψ_1 be the vector (with reduced dimension) of parameters other than ψ_1. Define

$$(5.27)\quad l_1(\psi_1) = \min_{\Psi_1} l(\psi_1, \Psi_1).$$

Then, based on the likelihood ratio test (Kendall and Stuart 1979, chapter 24), values of ψ_1 that solve the equation

$$(5.28)\quad l_1(\psi_1) = l(\hat{\Psi}) + \chi^2(1, p)$$

correspond to the end points of an approximate $100 \cdot p\%$ confidence interval for ψ_1.

Similarly, let (ψ_1, ψ_2) denote any pair of parameters in the vector Ψ, and let Ψ_2 be the (reduced) vector of parameters other than ψ_1 and ψ_2. Then the function

$$(5.29)\quad l_2(\psi_1, \psi_2) = \min_{\Psi_2} l(\psi_1, \psi_2, \Psi_2).$$

determines the boundary of a $100 \cdot p\%$ confidence region for (ψ_1, ψ_2) by the equation

$$(5.30)\quad l_2(\psi_1, \psi_2) = l(\hat{\Psi}) + \chi^2(2, p).$$

The concepts underlying (5.28) and (5.30) can be reversed. For example, given ψ_1 in (5.28), it is possible to solve for p. This means that, for each value of ψ_1, we can compute a probability level p for rejecting ψ_1 in favor of the estimate $\hat{\psi}_1$. We refer to the function $p(\psi_1)$ as a probability profile for ϕ_1. An example of such a profile is shown in our companion paper (Schnute et al. 1989, figure 4). In a similar fashion (5.30) can be used to compute a probability level p associated with (ψ_1, ψ_2). Contours of $p(\psi_1, \psi_2)$ correspond to confidence regions for (ψ_1, ψ_2).

As in our companion paper, we note that methods of inference other than (5.28) or (5.30) have been proposed (Edwards 1972). For example, one alternative would be to use the Hessian (a matrix of second derivatives) to determine an approximate covariance matrix for the parameters (Bard 1974, p. 176–179). By this method, confidence regions for (ψ_1, ψ_2) would always be ellipses centered on the estimate $(\hat{\psi}_1, \hat{\psi}_2)$. The method here may give nonelliptical regions situated asymmetrically around $(\hat{\psi}_1, \hat{\psi}_2)$. Such confidence regions in our example below have quite reasonable interpretations. Furthermore, recent research by Donaldson and Schnabel (1987) suggests that the Hessian method generally performs poorly in comparison with the method here.

The methods proposed here can be costly in computer time. A general minimization algorithm is required, both to compute the estimate $\hat{\Psi}$ from $l(\Psi)$ and to evaluate the functions $l_1(\psi_1)$ and $l_2(\psi_1, \psi_2)$ in (5.27) and (5.29). Furthermore, a single profile or contour plot requires many evaluations of l_1 or l_2, respectively. Just as our graphical analysis depends on modern spreadsheet software, so our statistical analysis is predicated on the availability of a good minimization algorithm. In our example below, we use a microcomputer implementation of the simplex search method (Nelder and Mead 1965; Press et al. 1986; Mittertreiner and Schnute 1985).

6. Special Cases

The statistical model (5.18) has been deliberately formulated in general terms, so that it can be tailored to a variety of contexts. As explained above, the example in section 5A serves as a prototype, but it lacks features required for realistic application here. In this section, we develop specific models for three categories of data: (i) fishery catch and CPUE data, along with associated size-frequency data, (ii) fishery catch and CPUE data alone, and (iii) tagged catch and CPUE data. In each case, we define a version of (5.18) and identify the associated process and measurement errors.

From [7] and (5.18), a model for fishery catch, CPUE, and size-frequency data is

$$(6.1)\quad (I_t^*)^{1/2} = [\sigma v_{t-1}(I_{t-1}^* - qC_{t-1}^*)]^{1/2} + \xi(\epsilon_t - \lambda\epsilon_{t-1}),$$

where, as usual, the variates ϵ_t are presumed normal with mean 0 and variance 1. We have already alluded to this model in the discussion following (5.18). A square root transform is used in (6.1) primarily because it produces relatively homoscedastic variance among model residuals. Also, we believe that this error structure reasonably reflects the precision of available data. The square root transform has been applied to catch, effort, and CPUE data in other fishery models (Kirkwood 1981; Quinn 1985).

By logic similar to that developed in (5.8)–(5.17), it can be shown that (6.1) corresponds to a family of models with combined process and measurement error. In analogy with (5.8), let ϕ^2 and ψ^2 denote variances associated with prediction and measurement, respectively, of the transformed CPUE $(I_t^*)^{1/2}$. For given parameters (σ, q), define the function

$$(6.2)\quad \zeta(\sigma, q) = \sqrt{\frac{\sigma\upsilon}{1 - qE}}$$

where υ and E are typical values of υ_t and E_t, respectively (such as the geometric means). Then, as proved in Appendix C, (6.1) is approximately equivalent to a combined process and measurement error model with

$$(6.3a)\quad \phi^2 = \xi^2 \cdot [\lambda - \zeta(\sigma, q)] \cdot \left[\lambda - \frac{1}{\zeta(\sigma, q)}\right],$$

$$(6.3b)\quad \psi^2 = \frac{\xi^2\lambda}{\zeta(\sigma, q)}.$$

In particular, the model has pure process error ($\psi = 0$) if $\lambda = 0$ and pure measurement error ($\phi = 0$) if

$$(6.4)\quad \lambda = \min\left[\zeta(\sigma, q), \frac{1}{\zeta(\sigma, q)}\right].$$

Notice the formal similarity between (5.16)–(5.17) and (6.3)–(6.4).

The model (6.1) requires size-frequency data for calculating the series υ_t. From [10] and (5.18), an analogous model for use without these data is

$$(6.5)\quad (I_t^*)^{1/2} = [A^* + \sigma(X'/X)\,(I_{t-1}^* - qC_{t-1}^*)]^{1/2} + \xi(\epsilon_t - \lambda\epsilon_{t-1}),$$

where the quantity X'/X is presumed known from sources external to the data. This model assumes constant recruitment, with an associated unknown parameter A^*.

Again, (6.5) corresponds to a family of models with combined sources of error. As before, let ϕ^2 and ψ^2 denote process and measurement errors for $(I_t^*)^{1/2}$. For given parameters (σ, q, A^*) define

$$(6.6)\quad \zeta(\sigma, q, A^*) = \frac{\sigma(X'/X)}{[(A^*/I^*) + \sigma(X'/X)\,(1 - qE)^{1/2}},$$

where I^* and E are typical values of I_t^* and E_t, respectively. Then it turns out (Appendix C) that measurement and process variances associated with (6.5) are approximately

$$(6.7a)\quad \phi^2 = \xi^2 \cdot [\lambda - \zeta(\sigma, q, A^*)] \cdot \left[\lambda - \frac{1}{\zeta(\sigma, q, A^*)}\right],$$

$$(6.7b)\quad \psi^2 = \frac{\xi^2\lambda}{\zeta(\sigma, q, A^*)}.$$

Furthermore, (6.5) corresponds to pure process error if $\lambda = 0$ and pure measurement error if

$$(6.8)\quad \lambda = \min\left[\zeta(\sigma, q, A^*), \frac{1}{\zeta(\sigma, q, A^*)}\right].$$

The similarity between (6.3)–(6.4) and (6.7)–(6.8) is obvious.

For the tag data we employ the model

$$(6.9a)\quad (I_1)^{1/2} = (qN_1)^{1/2} + \xi\epsilon_t,$$

$$(6.9b)\quad (I_t)^{1/2} = [\sigma(I_{t-1} - qC_{t-1})]^{1/2} + \xi\epsilon_t,$$

based on (3.5) and (3.6). The error in (6.9a) is essentially a measurement error associated with the CPUE I_1 in the first year of the experiment. By contrast, the error in (6.9b) is a pure process error ($\lambda = 0$) associated with the survival of tagged fish from one year to the next. Although a combined process and measurement error ($\lambda \neq 0$) would be desirable in (6.9b), there are too few years of available data for estimating λ, as well as σ and q. Another limiting feature of (6.9a)–(b) is the assumption that the error variance ξ^2 is the same in both equations. Again, although we would prefer a less restrictive assumption, the data are inadequate for estimating two variance parameters.

7. Illustrative Example: Graphics

7A. Data Sources

We illustrate the model with data from a lingcod stock off southwest Vancouver Island, British Columbia, Canada, in Pacific Marine Fisheries Commission (PMFC) Major Area 3C–N. The commercial trawl fishery accounts for the majority of lingcod catch in this area, although there are minor catches by hook and line fisheries. Here, we use the term catch to refer to reported catch, recognizing, for example, that discards may have occurred at sea. In addition to commercial fishery data, we use catch and effort data for 1982–86 recaptures of fish that had been tagged and released in Area 3C–N in 1982 (Table 4). The four data sets used in the analysis may be summarized as follows:

Data set	Time period
Fishery catch and effort	1956–86
Fishery sample weights	1956–86
Sample ages and weights	1977–85
Tag releases and recoveries	1982–86

Catch, effort, and biological sampling data from the commercial fishery used in the analysis are derived from several sources. We detail these sources and compilation procedures in a separate report (Cass et al. 1988), and only the essential features of the

TABLE 4. Numbers of released and recaptured fish and corresponding recapture fishing efforts (E_t, 10^3 h) by the 25% and Option-2 methods, for marked lingcod from Area 3C–N, 1982–86.

	Number of fish		Effort	
Year	Released	Recaptured	25%	Option-2
1982	7501	1445	2.701	2.289
1983	0	727	3.507	3.324
1984	0	252	4.581	3.685
1985	0	164	7.364	7.089
1986	0	19	3.127	2.870

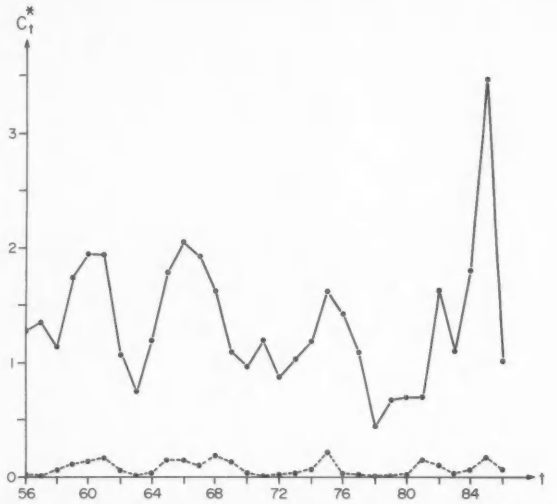

FIG. 1. Time series of all-gear adjusted catch C_t^* (10^3 t) (solid line) and prerecruit catch (dashed line) for Area 3C–N lingcod. Year t ranges from 1956–86, as indicated by the last two digits.

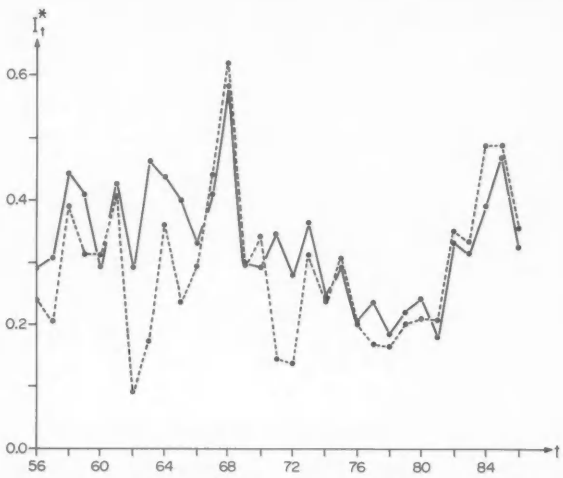

FIG. 2. Time series of CPUE I_t^* ($t \cdot h^{-1}$) for Area 3C–N lingcod. CPUE is calculated by the 25% method (solid line) and the Option-2 method (dashed line). Year t ranges from 1956–86.

data are presented below. Sample ages are based on the fin-ray method of age determination (Beamish and Chilton 1977).

The lingcod trawl fishery is part of a multispecies fishery that also targets on Pacific cod (*Gadus macrocephalus*), petrale sole (*Eopsetta jordani*), and occasionally other species. Calculation of CPUE for a multispecies fishery depends on the way in which fishing effort is assumed to be partitioned among species. Various practitioners have expressed preference for certain of these methods. To examine the effect of the calculation method, we compare model results from two methods of CPUE calculation.

Catch and effort data from the commercial fishery on the Area 3C–N lingcod stock have been recorded since 1956. Between 1956–86, 91% of the Canadian lingcod catch from Area 3C–N occurred during May–September. To ensure that our estimate of CPUE is representative, CPUE is based on trawl landings for the May–September fishing period only. For the first method of CPUE calculation, termed 25%, the lingcod catch and total effort from a landing are included in the analysis only if lingcod account for 25% or more of the catch by weight. The second method is the Option-2 method of Westrheim (1983). For this method, CPUE is based on catch and effort from the two depth intervals that account for the majority of the lingcod catch. In both methods, we further standardize effort for variation in vessel fishing power according to Westrheim and Foucher (1985).

The biological sampling data provide annual estimates of the size-frequency distribution of the trawl catch. These data are introduced in our companion paper (Schnute et al. 1989). There we discuss steps 1–2 in the graphical analysis of size-frequency data, that is, estimation of the parameters V, V', and ρ, and the population weight means X_t, Y_t, and Z_t (Schnute et al. 1989, figure 6). The final values obtained in our companion paper (Schnute et al. 1989, equations (3.6)–(3.7)) are applied directly here. As suggested in step 2, we repeat the entire analysis to examine the consequences of uncertainty in V'. We use V = 2.25 kg, and both the estimate

(7.1) $\hat{V}' = 2.88$ kg, $\hat{\rho} = 1.025$,

and the extreme value of V'

(7.2) $V' = 3.50$ kg, $\hat{\rho} = 1.024$.

The estimates $\hat{\rho}$ appear to be roughly independent of V'. We refer to (7.1)–(7.2) by the value of V' only, and the corresponding estimates $\hat{\rho}$ are always assumed in the discussion below.

7B. Analysis with Size–Frequency Data

Section 4 outlines a procedure for estimating the total survival τ in a stable fishery. This procedure uses the entire weight-frequency distribution ($w \geq V$), but requires the distribution to be averaged over years. The average weight-frequency distribution is shown in figure 1 of our companion paper (Schnute et al. 1989). We use these data to obtain the observed cumulative weight distribution $\hat{\Theta}(w)$, beginning at weight V. A general minimization algorithm is required to estimate τ from $\kappa(\tau)$ in (4.12), and we use the methods discussed earlier at the end of section 5.

Following these procedures, $\kappa(\tau)$ is minimized at $\hat{\tau} = 0.78$ when $V' = 2.88$ kg, and $\hat{\tau} = 0.62$ when $V' = 3.50$ kg. Corresponding minimum values for $\kappa(\tau)$ are 0.041 and 0.037, respectively. These estimates $\hat{\tau}$ provide a baseline for comparison with results obtained below from the annual fishery data. Incidentally, for a test at the 0.05 significance level, the critical value of $\kappa(\tau)$ is 0.036 (Kendall and Stuart 1979, p. 481), based on the average annual sample size of 1391 measurements. Although the minimum values obtained for $\kappa(\tau)$ are slightly greater than the critical value, this is not unexpected due to a departure of the observed data from the theoretical model. In (4.4), $\theta(w)$ is a decreasing function of w. The observed distribution of $\theta(w)$ has an ascending limb in the region near V. This results from partial recruitment of fish of weight near V to the fishery. For both $V' = 2.88$ kg and $V' = 3.50$ kg, the value of $|\Theta(w; \hat{\tau}) - \hat{\Theta}(w)|$ is maximum when w corresponds to the weight interval that begins at V.

Graphical analysis using the annual size-frequency data follows the procedure outlined in section 2A. Starting with step 3, the catch C_t^* is adjusted downward to account for the pre-

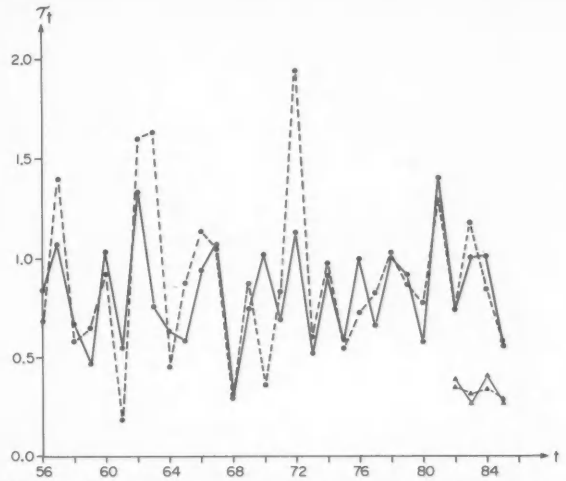

FIG. 3. Time series τ_t for fishery data compiled with $V' = 2.88$ kg (circles), and for tag data (triangles). CPUE is calculated by the 25% method (solid lines), and the Option-2 method (dashed lines). Year t ranges from 1956–85 for fishery data and from 1982–85 for tag data.

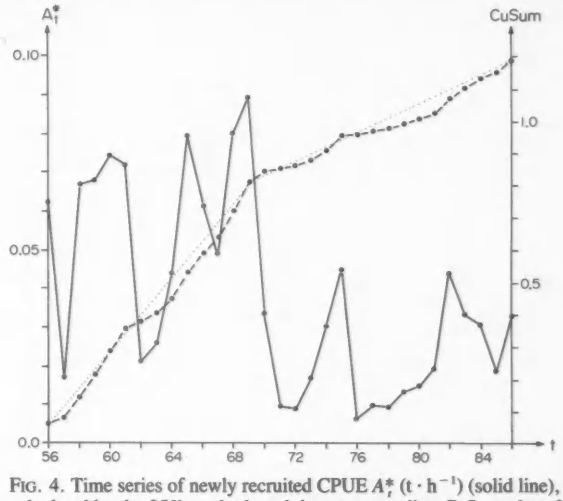

FIG. 4. Time series of newly recruited CPUE A_t^* ($t \cdot h^{-1}$) (solid line), calculated by the 25% method, and the corresponding CuSum plot of A_t^* (dashed line). Thin dashed lines represent trends on the CuSum plot associated with the means from 1956–69 and 1969–86. Data are compiled with $V' = 2.88$ kg, and year t ranges from 1956–86.

TABLE 5. Preliminary estimates $\hat{\tau}$ and corresponding ranges for the total survival τ. Estimates from the equilibrium model are obtained by minimizing $\kappa(\tau)$ in (4.12). Dynamic model estimates are geometric means of the series τ_t, calculated from either (2.3) for fishery data or (3.7) for tag data. The corresponding ranges indicate observed low and high values of τ_t in each series. Where possible, results are presented for two methods of calculating CPUE and two values of V'.

Model	Data source	CPUE	V' (kg)	$\hat{\tau}$	τ Range
Equilibrium	Fishery	—	2.88	0.78	—
Dynamic	Fishery	25%	2.88	0.78	0.31–1.39
Dynamic	Fishery	Option 2	2.88	0.78	0.18–1.94
Equilibrium	Fishery	—	3.50	0.62	—
Dynamic	Fishery	25%	3.50	0.60	0.20–1.10
Dynamic	Fishery	Option 2	3.50	0.61	0.15–1.69
Dynamic	Tag	25%	—	0.33	0.27–0.40
Dynamic	Tag	Option 2	—	0.32	0.29–0.35

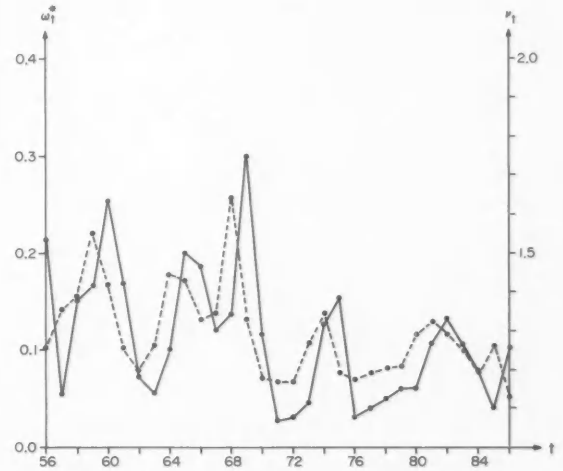

FIG. 5. Time series ω_t^* (solid line), and υ_t (dashed line), for data compiled with $V' = 2.88$ kg. Year t ranges from 1956–86.

recruit catch, the catch of fish of weight less than V. As in step 4, the CPUE for each year, I_t^*, is calculated as the ratio of adjusted catch from selected landings to standardized effort. In this case, the raw data include C_t^* and I_t^*, rather than C_t^* and E_t. Hence, total effective effort E_t is calculated from (2.2). The remaining quantities required for the analysis, ω_t^*, A_t^*, τ_t and υ_t, are obtained as described in steps 4–5.

Step 6 in the analysis involves time series and CuSum plots of C_t^*, E_t, X_t, Y_t, Z_t, I_t^*, A_t^*, ω_t^*, τ_t, and υ_t. To investigate the method of CPUE calculation, we repeat plots of E_t, I_t^*, A_t^*, and τ_t for the 25% and Option-2 methods. Also, to investigate the effect of V', we repeat plots of A_t^*, ω_t^*, τ_t and υ_t for $V' = 2.88$ kg and $V' = 3.50$ kg. Thus, we obtain four versions of the plots for A_t^* and τ_t, associated with two values of V' and two measures of CPUE. We discuss the principal features of these plots below, using CPUE calculated by the 25% method with $V' = 2.88$ kg for illustration in most cases.

The catch C_t^* (Fig. 1) varies consistently within the range 440–2040 t over the period 1956–86, with the exception of 1985 when C_t^* has a value of 3452 t. The prerecruit catch, the biomass excluded from C_t^* in step 3, is small and varies between 9–225 t. The time series I_t^* is similar for the 25% and Option-2 methods (Fig. 2). In general, the Option-2 method tends to accentuate the highs and lows in the series. The highest value of I_t^* occurs in 1968 for both methods, and there is an extreme low value in 1962 for the Option-2 method.

The difference in variability between the 25% and Option-2 methods is also evident from plots of τ_t (Fig. 3). The range in τ_t is more extreme for the Option-2 method, although both methods give estimates $\tau_t > 1$ for some years t. Individual values τ_t outside the interval (0, 1) are perhaps inevitable in the context of noisy fishery data; nevertheless, the plot can still be used to assess overall variation in survival. In Fig. 3, there are no apparent time trends. Furthermore, the geometric mean of each series τ_t lies in the interval (0, 1), and these means are

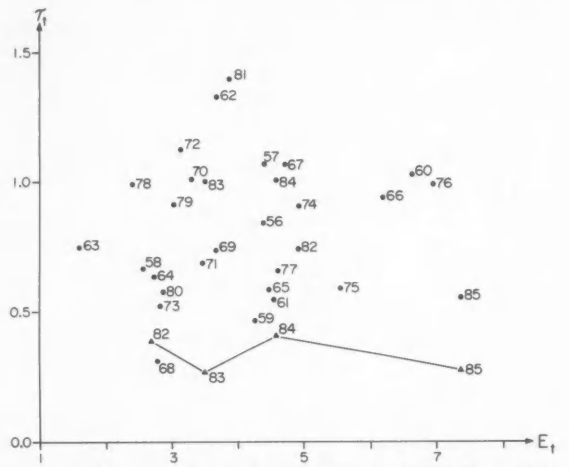

FIG. 6. Scatter plot of the relationship between τ_t and E_t (10^3 h). CPUE is calculated by the 25% method. Circles indicate fishery data compiled with $V' = 2.88$ kg, and connected triangles indicate tag data. Year t is indicated by a two digit label so that, for example, "60" refers to 1960.

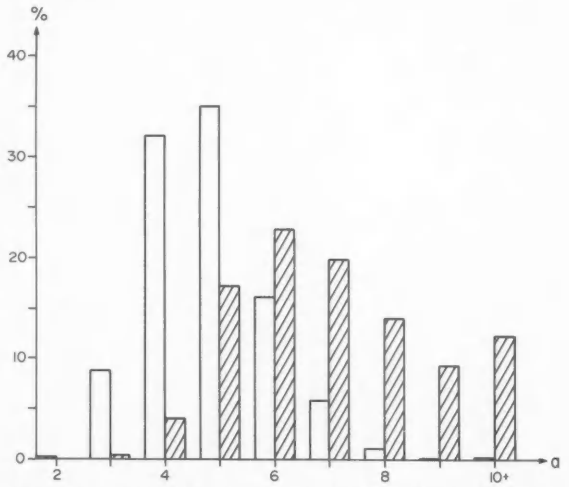

FIG. 7. Percentage of biomass at age a in the newly recruited population (open bars) and previously exploited population (striped bars). Percentages are based on the annual age distribution, averaged over the period 1977–85. The last interval includes all fish of age 10 or greater.

similar for each CPUE method for a given V' (Table 5). The geometric mean of τ_t is lower with $V' = 3.50$ kg than with $V' = 2.88$ kg. Survival must be reduced to compensate for a higher level of recruitment associated with a broader weight interval (V, V').

For both CPUE methods and V' values, the geometric means of τ_t are similar to corresponding estimates $\hat{\tau}$ obtained from the equilibrium model above (Table 5). This similarity is remarkable as the equilibrium model estimates are obtained without CPUE data. Instead, they depend on the entire weight distribution averaged over time. By contrast, the geometric means depend on the entire time series of CPUE data and only the annual means of the weight distribution. The similarity between

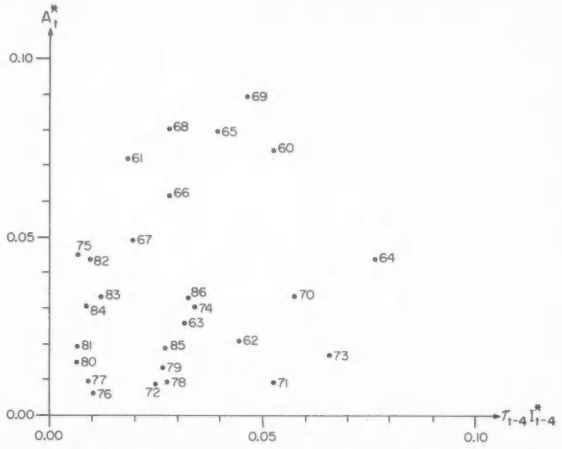

FIG. 8. Scatter plot of the relationship between A^*_t ($t \cdot h^{-1}$) and $\tau_{t-4}I^*_{t-4}$ for fishery data compiled with $V' = 2.88$ kg. CPUE is calculated by the 25% method. Year t is indicated by a two digit label.

TABLE 6. For given values of A^* (t/h), two estimates $\hat{\tau}$ of τ from the analysis without size-frequency data, using $V' = 2.88$ kg. The first estimate ("Linear") is linearly related to A^* by (2.7) and (7.4a). The second estimate ("GM") is the geometric mean of the series τ_t obtained from (2.9) for the given value of A^*. The GM estimate is missing for $A^* = 0.20$ t/h, as a few values of τ_t are negative in this case.

	$\hat{\tau}$	
A^*	Linear	GM
0.00	0.87	0.88
0.05	0.74	0.74
0.10	0.60	0.58
0.15	0.46	0.44
0.20	0.33	—

models is possibly due to the fact that q appears to be small, as shown below. When q is small, $\tau \simeq \sigma$ and τ is no longer time variant.

The time series plots of A^*_t (Fig. 4), ω^*_t and υ_t (Fig. 5) appear somewhat similar. For all three plots, there is an apparent break in the series near 1969, and values are generally lower and less variable for the later part of the series. The CuSum plots of ω^*_t and A^*_t (Fig. 4) are the only ones to show any evidence of an intervention. For both plots, the slope of the CuSum trend decreases after 1969. Compiling the data with $V' = 3.50$ kg results in higher estimates of Y_t, and consequently higher values of A^*_t, ω^*_t and υ_t. Otherwise, the patterns in these plots are similar to those obtained with $V' = 2.88$ kg. In our concluding remarks (section 9), we discuss possible reasons for an intervention in ω^*_t and A^*_t.

Step 7 involves plots of τ_t versus E_t (Fig. 6), that should by [5] have an intercept σ and slope $-\sigma q$. For all four possible plots, no relationship between τ_t and E_t is evident visually. Since τ_t appears to be independent of E_t, q appears small. Even the highest value of E_t ($t = 1985$) does not result in a particularly low value of τ_t, and moderate values of E_t (3–5 $\times$ 10^3 h) result in a wide range of survivals τ_t. Thus, the fishery appears to have little effect on stock survival, and noise in the data masks any effect that may exist. Note that, if $q = 0$, then the mean of τ_t is an estimate of σ.

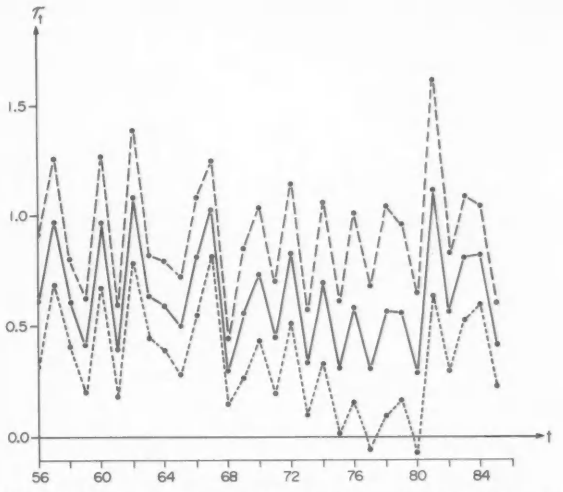

FIG. 9. Time series τ_t obtained from (2.9) using three values for A^* ($t \cdot h^{-1}$): $A^* = 0.0$ (long dashed line), $A^* = 0.1$ (solid line), and $A^* = 0.2$ (short dashed line). CPUE is calculated by the 25% method. Year t ranges from 1956–85.

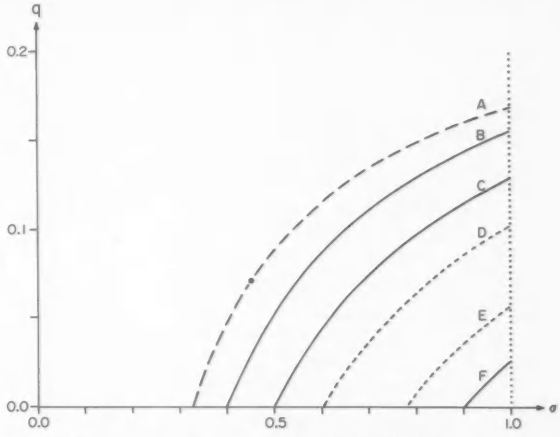

FIG. 10. Contour lines for the relationship (4.11) between q and σ, where $E = 3.98 \times 10^3$ h for tag data and $E = 3.88 \times 10^3$ h for fishery data, the geometric means of effort E_t from the 25% method. Each contour line corresponds to a specific value of τ as follows: (A) $\tau = 0.33$, an estimate from the tag data, (B) $\tau = 0.40$, (C) $\tau = 0.50$, (D) $\tau = 0.60$, an estimate from the fishery data with $V' = 3.50$ kg, (E) $\tau = 0.78$, an estimate from the fishery data with $V' = 2.88$ kg, and (F) $\tau = 0.90$. Corresponding values of A^* ($t \cdot h^{-1}$) on these contours from (7.4a) are (A) $A^* = 0.20$, (B) $A^* = 0.17$, (C) $A^* = 0.14$, (D) $A^* = 0.10$, (E) $A^* = 0.03$, and (F) $A^* = -0.01$. The circle represents the tag estimate (7.6).

As described earlier, 1982–86 catch and effort data are available for lingcod tagged in 1982 (Table 4). Where applicable, tag data have been included on plots of the fishery data discussed above (Fig. 3 and 6). Estimates of τ_t for the tag data cover a narrow range (Fig. 3), and are considerably lower than for the fishery data (Table 5). In the plot of τ_t versus E_t (Fig. 6), a slight decreasing trend is apparent. In contrast with the fishery data, the tag data provide a direct estimate $\hat{q}$ of q. From (3.5), $\hat{q} = 0.071 \times 10^{-3}\ h^{-1}$ for the 25% method and $\hat{q} = 0.084 \times 10^{-3}\ h^{-1}$ for the Option-2 method. Corresponding estimates $\hat{\sigma}$ of σ from the geometric mean of the ratios $I_{t+1}/(I_t - qC_t)$ are $\hat{\sigma} = 0.49$ and $\hat{\sigma} = 0.50$ for the two CPUE methods, respectively.

It is apparent from these results that σ is lower and q higher for the tag data than for the fishery data. This result contrasts with the result in our companion paper (Schnute et al. 1989) that tagged fish share growth parameters with the entire population. There are several obvious reasons why tagged fish might have survival and catchability parameters different from those of the underlying population. For example, our model does not account for mortality due to tagging, for tag loss, or for nonreporting of tags. We discuss such possibilities further in section 9.

To investigate recruitment as described in step 8, we first examine the proportion of biomass by age in the newly recruited and previously exploited populations (Fig. 7), where the data come from the limited age samples cited in section 7A. The proportion of biomass at age a in the newly recruited population is an estimate for π_a. Here, π_a is maximum for $a = 5$, although π_4 is similar in value to π_5. We select age-4 recruitment for illustration, as age-5 fish comprise the youngest abundant age in the previously exploited population. There is no apparent relationship between A_t^* and $\tau_{t-4}I_{t-4}^*$ for any of the four possible combinations of V' and CPUE method (Fig. 8), or between A_t^* and $\tau_{t-a}I_{t-a}^*$ for other ages. Once again, noise in the data appears to mask any relationship that may exist. As discussed in connection with (2.4), our information on the stock does not improve our prediction of recruitment beyond a prediction based on the mean alone. Consequently, in our statistical application of [8] below, we confine our attention to a single parameter A^* associated with constant recruitment. Again, we stress that this does not imply the absence of a stock–recruitment relationship, merely the lack of evidence for one.

7C. Analysis without Size–Frequency Data

If historical size-frequency data are not available, then graphical analysis follows the steps outlined in section 2B. For illustration, we discuss the case with the 25% method of CPUE calculation. In step 1, we estimate $X = 4.72$ kg from the geometric mean of X_t. Then from (1.6) and (1.12) we obtain the estimates

$$(7.3)\quad X'/X = \begin{cases} 1.15, & V' = 2.88 \text{ kg}, \\ 1.28, & V' = 3.50 \text{ kg}, \end{cases}$$

depending on the chosen value of V' in (7.1)–(7.2). Estimates of I_t^*, C_t^*, and E_t in step 2 are identical to the analysis with size-frequency data. The geometric mean of I_t^* is 0.319 t/h, from which (2.7) gives the linear relationship

$$(7.4a)\quad A^* = 0.319 - 0.367\,\tau,$$

for $V' = 2.88$ kg, or equivalently

$$(7.4b)\quad \tau = 0.869 - 2.72\,A^*.$$

We use $V' = 2.88$ kg only for illustration below. Note that the increase in V' from 2.88 kg to 3.50 kg results in an increase in X'/X of about 11%. For a given A^*, the estimate for τ will be reduced by this amount for $V' = 3.50$ kg relative to $V' = 2.88$ kg.

Possible estimates of A^* and τ can be obtained as described in step 4. From a plot (not shown here) of the relationship

TABLE 7. Examples used to illustrate the statistical analysis, along with corresponding model equations. Each example is characterized by a data source (fishery or tag data), a CPUE calculation method (25% or Option-2), the use of size-frequency data (yes or no), a value of V' (the estimate 2.88 kg or the extreme 3.50 kg), and an error structure (process and measurement combined, process alone, or measurement alone). Analysis of each example depends on the additional parameters shown, where ρ and X'/X are given by (7.1) and (7.3), respectively. Values of E (10^3 h), υ, and I^* (t/h) are geometric means of the corresponding data series E_t, υ_t, and I_t^* for each example.

							Additional parameters				
No.	Model	Source	CPUE	Size?	V'	Error	ρ	E	υ	I^*	X'/X
1	(6.1)	Fishery	25%	Yes	2.88	Combined	1.025	3.88	—	—	—
2	(6.1)	Fishery	25%	Yes	2.88	Process	1.025	3.88	—	—	—
3	(6.1)	Fishery	25%	Yes	2.88	Measurement	1.025	3.88	1.29	—	—
4	(6.1)	Fishery	25%	Yes	3.50	Combined	1.024	3.88	—	—	—
5	(6.1)	Fishery	25%	Yes	3.50	Process	1.024	3.88	—	—	—
6	(6.1)	Fishery	25%	Yes	3.50	Measurement	1.024	3.88	1.67	—	—
7	(6.5)	Fishery	25%	No	2.88	Combined	—	3.88	—	—	1.15
8	(6.5)	Fishery	25%	No	2.88	Process	—	3.88	—	—	1.15
9	(6.5)	Fishery	25%	No	2.88	Measurement	—	3.88	—	0.319	1.15
10	(6.5)	Fishery	25%	No	3.50	Combined	—	3.88	—	—	1.28
11	(6.5)	Fishery	25%	No	3.50	Process	—	3.88	—	—	1.28
12	(6.5)	Fishery	25%	No	3.50	Measurement	—	3.88	—	0.319	1.28
13	(6.1)	Fishery	Option-2	Yes	2.88	Combined	—	3.88	—	—	—
14	(6.9)	Tag	25%	—	—	—	1.025	3.98	—	—	—

TABLE 8. Parameter estimates for the 14 examples listed in Table 7, along with corresponding minimum values of the likelihood function l. Values of $\tau = \sigma(1 - qE)$ from (4.11) are also shown, where corresponding values of E are listed in Table 7. For models with size-frequency data, values of A^* (shown in parentheses) are geometric means of the series A_t^* from (1.26). For models with combined measurement and process error, the ratios ψ/ϕ are shown. The parameter q is designated "0" in cases where the estimate lies on the constraint $q = 0$. Similarly λ, ϕ, and ψ are designated "0" when the error structure requires a constraint to the value zero. The parameters σ and λ are dimensionless, while q and A^* have units $10^{-3}\ \text{h}^{-1}$ and t/h, respectively. The error standard deviations ξ, ϕ, and ψ each have units $(\text{t/h})^{1/2}$.

No.	σ	q	τ	A^*	λ	ξ	ϕ	ψ	ψ/ϕ	l
1	0.760	0	0.760	(0.030)	0.477	0.090	0.047	0.063	1.3	−41.92
2	0.740	0	0.740	(0.030)	0	0.100	0.100	0	—	−36.28
3	0.967	0.053	0.768	(0.030)	0.796	0.111	0	0.088	—	−29.04
4	0.569	0	0.569	(0.065)	0.283	0.113	0.081	0.061	0.8	−28.90
5	0.555	0	0.555	(0.065)	0	0.116	0.116	0	—	−27.27
6	0.837	0.076	0.590	(0.065)	0.711	0.146	0	0.104	—	−12.70
7	0.706	0	0.706	0.062	0.459	0.070	0.036	0.053	1.5	−56.23
8	0.358	0	0.358	0.191	0	0.073	0.073	0	—	−54.15
9	0.813	0	0.813	0.018	0.937	0.075	0	0.075	—	−50.18
10	0.633	0	0.633	0.062	0.459	0.070	0.036	0.053	1.5	−56.23
11	0.321	0	0.321	0.191	0	0.073	0.073	0	—	−54.15
12	0.729	0	0.729	0.018	0.937	0.075	0	0.075	—	−50.18
13	0.759	0	0.759	(0.030)	0.406	0.132	0.078	0.084	1.1	−19.36
14	0.455	0.071	0.326	—	—	0.018	—	—	—	−32.25

between I_{t+1}^* and $(X'/X)I_t^*$, it appears that a reasonable range for the intercept A^* is between 0–0.20 t/h. From (7.4b), this range in A^* corresponds to the range 0.33–0.87 for τ (Table 6). We can contrast this uncertainty in A^* and τ with the estimates

(7.5a) $\hat{A}^* = 0.03$ t/h,

(7.5b) $\hat{\tau} = 0.78$,

obtained from the geometric mean of the series A_t^* and τ_t computed using size-frequency data with $V' = 2.88$ kg. In fact, the point (7.5) turns out to lie nearly on the line (7.4). The benefit of size-frequency data is obvious. These data help resolve the distinction between recruitment and survival. With A^* unknown, the estimation of τ is much less certain.

Following steps 5–6, we obtain time series plots of τ_t with A^* fixed at 0.0 t/h, 0.1 t/h, and 0.2 t/h (Fig. 9). We note that

the low value of A^* gives numerous values of τ_t greater than 1 and that the high value of A^* gives a series τ_t often less than 0. Thus, the proposed range of A^* appears to bracket the range of possibilities reasonably. Similarly, we obtain plots of A_t^* with τ fixed at the three values (0.87, 0.60, and 0.33, respectively, in Table 6) corresponding to the three choices of A^*. These plots (not shown) are not particularly revealing. For example, the decrease in A_t^* over time that was observed with the size-frequency data is not apparent here. In general, there are no apparent breaks in corresponding CuSum plots of A_t^* or τ_t. Incidentally, Table 6 shows a measure of self-consistency in this analysis. For a given value of A^*, the geometric mean τ of the corresponding series τ_t from (2.9) agrees favorably with the value of τ obtained from (7.4b).

The plots of τ_t versus E_t for step 7 are not suggestive of a negative relationship. At best, the relationship is constant or increasing. Similarly, there appears to be no evidence of a stock–recruitment relationship. As in the earlier analysis with size-frequency data, the plots of A_t^* versus τI_{t-4}^* for step 8 suggest that recruitment is independent of stock size.

7D. Analysis of σ and q

If effort is assumed to be constant, a relationship between q and σ is defined by (4.11). This provides a convenient device for investigating the implications of various estimates of τ from graphical analysis. If CPUE is calculated by the 25% method, we estimate $E = 3.88 \times 10^3$ h for the fishery data and $E = 3.98 \times 10^3$ h for the tag data, from the geometric mean of E_t over the corresponding time periods. With these values of E, (4.11) implies that, for each τ, values of σ and q lie on a hyperbola in σq-space. Hyperbolas for various estimates of τ are shown as contour lines in Fig. 10. Note that boundaries of the contours result from the constraints (1.16)–(1.17). At $\tau = 1$, the maximum value of τ, the contour reduces to the point $(\sigma, q) = (1, 0)$. Smaller values of τ give longer contours. Furthermore, by (7.4), each contour also corresponds to a value of A^*, where smaller values of A^* give shorter contours.

The longest contour in Fig. 10 corresponds to $\tau = 0.33$, the geometric mean of the series τ_t for the tag data. The position of q on this contour can be estimated from (3.5), and the corresponding point

$$(7.6) \quad (\hat{\sigma}, \hat{q}) = (0.455, 0.071 \times 10^{-3}\ \mathrm{h}^{-1})$$

is shown in Fig. 10. If no size-frequency data are available for the fishery, the contours depend on the estimate of A^* from which τ is calculated. Thus,values of τ cover the potentially wide range 0.33–0.87 cited above. By contrast, if size-frequency data are available, τ is relatively well determined. For example, corresponding to the estimate $V' = 2.88$ kg, we estimate $\tau = 0.78$ (Table 5). Thus, we would conclude that the point (σ, q) lies roughly on the contour (E) in Fig. 10. Without the size-frequency data, we would only conclude that (σ, q) must lie somewhere in the broad range of contours from (A) to (F).

8. Illustrative Example: Statistics

So far, we have obtained estimates and approximate confidence intervals for σ and q using graphical techniques. With these as a guide, we next present results from statistical analysis. We illustrate this analysis with a total of 14 examples (Table 7). The first six relate to model (6.1), with two choices

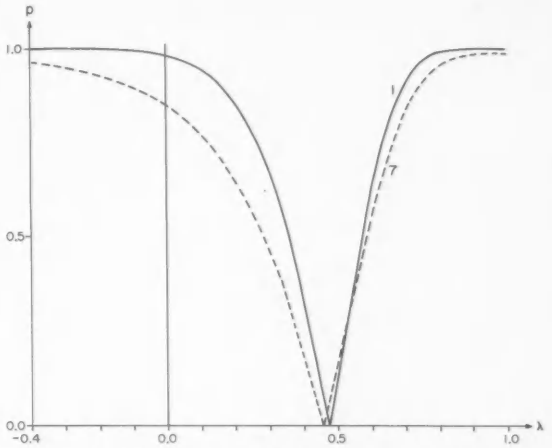

FIG. 11. Probability profiles $p(\lambda)$ for examples 1 (solid line, size-frequency data) and 7 (dashed line, no size-frequency data).

of V' and three choices of error structure. Similarly, the next six examples relate to model (6.5). Together, the first 12 examples represent two choices of V', three possible error structures, and two alternatives for size-frequency data (included or not). Of these 12, we consider example 1 to be the most credible, and examples 13–14 are chosen to be comparable with example 1. In example 13, CPUE is calculated by the Option-2 method, rather than the 25% method used in examples 1–12. Example 14 corresponds to model (6.9) for the tag data. Notice that no alternatives associated with size-frequency data, V', or error structure are relevant to the tag data.

The examples referenced in Table 7 have various data requirements. All of them require catch and CPUE data, and, except for example 12, we consistently use the 25% method of calculating CPUE. Furthermore, to obtain comparable results, we convert the Option-2 CPUE data in example 12 to equivalent 25% CPUE units. The scale factor for this conversion is chosen so that the converted Option-2 series has the same geometric mean as the 25% series.

Examples 1–6 and 13, based on (6.1), also require the series v_t, which is calculated from [1] and [2] using the series X_t, Y_t, Z_t, and X'_t. Thus, these examples depend on the growth parameters (V', ρ) in two ways. First, the value of V' is used in compiling historical sample data to obtain the means Y_t and Z_t. Second, both V' and ρ are used to compute X'_t from X_t. Values of ρ appropriate to the two choices for V' are given in (7.1)–(7.2) and are also listed in Table 7. Examples 7–12, based on (6.5), similarly depend on (V', ρ). In this case, however, the growth parameters influence only the calculation of X'/X, as shown in (7.3) and Table 7.

Examples 3 and 6 involve the constraint (6.4) that defines the case of pure measurement error for model (6.1). Values of E and v are required to compute λ from (6.4); these are taken to be the geometric means of the series E_t and v_t (Table 7). Similarly, examples 9 and 12 involve the constraint (6.8), which requires values of E, I^*, and X'/X. Again, choices of these parameters are indicated in Table 7.

Parameter estimates for (6.1), (6.5),and (6.9) are obtained by following the steps outlined in section 5B. For each model, the corresponding likelihood function (5.25) is minimized, subject to the constraints (1.16), (1.17), and (2.4b) for σ, q, and A^*, respectively. A general minimization algorithm is neces-

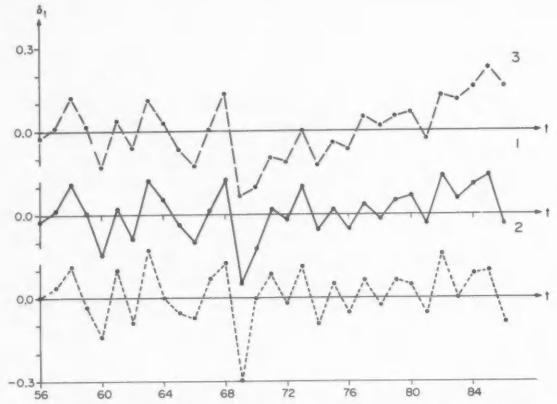

FIG. 12. Time-series of residuals δ_t ($t \cdot h^{-1}$) for examples 1 (solid line, $\hat{\lambda} = 0.477$), 2 (short dashed line, $\lambda = 0$), and 3 (long dashed line, $\hat{\lambda} = 0.796$), to compare the effects of combined, process, and measurement errors.

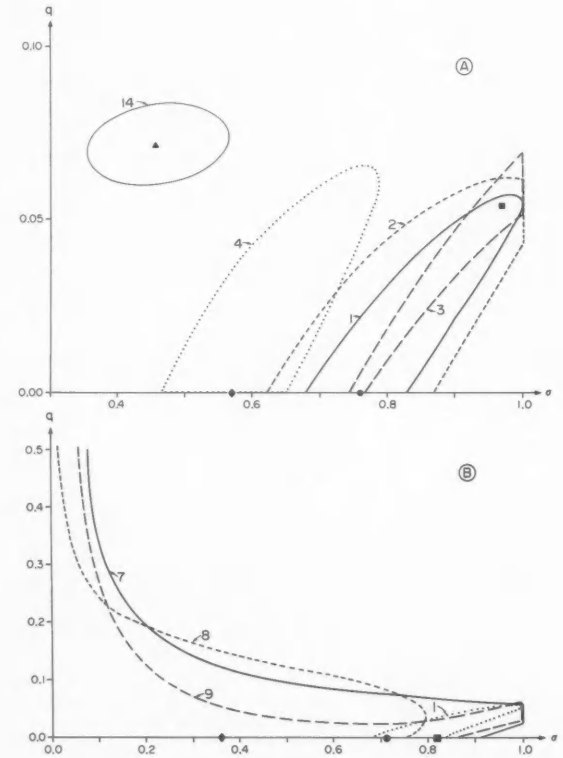

FIG. 13. (A) Approximate 95% confidence regions for (σ, q) obtained for examples 1 (solid line), 2 (short dashed line), 3 (long dashed line), 4 (dotted line) and 14 (thin line). Corresponding point estimates are shown for examples 1 (circle), 3 (square), 4 (diamond), and 14 (triangle). (B) Approximate 95% confidence regions and point estimates for (σ, q) obtained for examples 7 (solid line, circle), 8 (short dashed line, diamond), and 9 (long dashed line, square). Example 1 (dotted line) is included for reference.

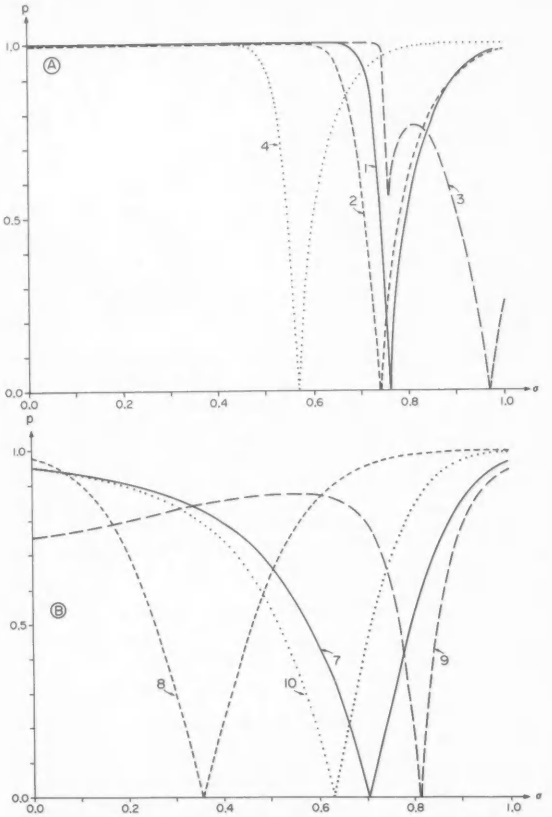

FIG. 14. Probability profiles $p(\sigma)$ obtained for (A) examples 1 (solid line), 2 (short dashed line), 3 (long dashed line) and 4 (dotted line), and (B) examples 7 (solid line), 8 (short dashed line), 9 (long dashed line) and 10 (dotted line).

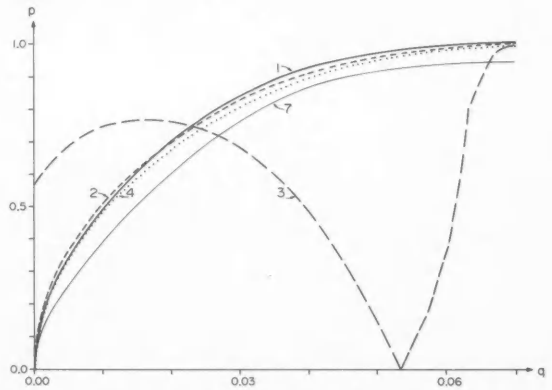

FIG. 15. Probability profiles $p(q)$ obtained for examples 1 (solid line), 2 (short dashed line), 3 (long dashed line), 4 (dotted line), and 7 (thin line).

sary, and we apply the methods discussed at the end of section 5C. Table 8 lists parameter estimates for the 14 examples discussed above. In each case, estimates of σ and q are used to compute $\tau = \sigma(1 - qE)$ from (4.11), using the corresponding

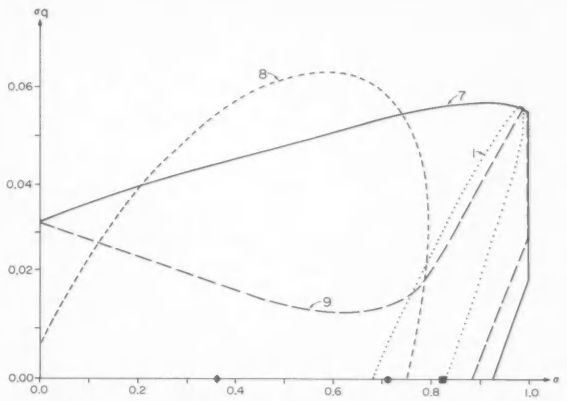

FIG. 16. Approximate 95% confidence regions and point estimates for $(\sigma, \sigma q)$ obtained for examples 7 (solid line, circle), 8 (long dashed line, diamond), and 9 (short dashed line, square). Example 1 (dotted line) is included for reference.

value of E in Table 7. Similarly, ϕ and ψ are calculated from (6.3) for examples 1–6 and from (6.7) for examples 7–12. Various results from the statistical analysis compare favorably with graphical results earlier. For instance, estimates of τ for examples 1, 4, and 14 in Table 8 agree closely with comparable estimates in Table 5. Furthermore, estimates of σ and q from the tag data (example 14) are identical to the graphical estimates (7.6). In particular, both graphical and statistical analyses agree that tag data and fishery data lead to distinctly different estimates of survival parameters.

We discuss Table 8 in detail by comparing rows and sets of rows, using example 1 as a benchmark. We regard example 1 as the most plausible for the fishery data, since it includes combined error structure, size-frequency data, and the estimate $\hat{V}'$ of V' from our companion paper (Schnute et al. 1989). Our opinion is supported by the fact that example 1 gives the best fit (lowest l) among comparable examples 1–6.

Example 2 has estimates similar to example 1, but has a poorer overall fit. Values of l for examples 1 and 2 can be compared using the χ^2 statistic with 1 *df*. By this method, the null hypothesis of pure process error ($\lambda = 0$) can be rejected against the alternative hypothesis of combined error ($\lambda \neq 0$) with 98% confidence:

$$(8.1) \quad -36.28 - (-41.92) \simeq \chi^2(1, 0.98).$$

In fact, estimates of ψ and ϕ for example 1 suggest that measurement error exceeds process error ($\psi > \phi$). Pure measurement error in example 3, however, leads to an even poorer fit than pure process error. The estimates of σ and q for example 3 are also very different from examples 1 and 2, although the estimate of τ is similar.

Examples 1–3 illustrate a fundamental point: the assumed error structure can profoundly influence a model's conclusions. (See Schnute 1987b, especially section 2, for an extensive discussion.) If we assume pure process error (example 2), we conclude that mortality is primarily due to natural processes ($\sigma = 0.74$) and hardly affected by fishing ($q = 0$). On the other hand, assuming pure measurement error, we conclude that there is little natural mortality ($\sigma = 0.97$) and that most mortality occurs from fishing ($q = 0.053$ and $1 - qE = 0.79$). Our general model allows us to reject both these error structures in favor of a combined error (example 1), and we conclude that the scenario indicated by process error is closer to the truth in this case.

Parameter estimates for examples 4–6 vary with error structure in a manner analogous to examples 1–3. The higher value of V' results in lower estimates of τ, as expected from graphical analysis (Table 5). Note, however, the considerably poorer fit of examples 4–6, and the correspondingly higher estimates of ξ. This overall poor fit for examples 4–6 supports our choice of V' in examples 1–3. The ratio ψ/ϕ for example 4 suggests a bias towards pure process error ($\psi < \phi$). In fact, given that $V' = 3.50$ kg, the hypothesis of pure process error (example 5) cannot be rejected against combined error (example 4) with 95% confidence. By contrast, pure measurement error (example 6) can be rejected with a very high level of confidence.

Parameter estimates for example 7 are similar to the estimates for example 1. Comparison of examples 7–9, however, shows that the assumed error structure radically influences the estimates of σ and τ when size-frequency data are not used. In particular, pure process error (example 8) leads to survival estimates that are far too low. Conversely, pure measurement error gives estimates that are too high.

Example 8 represents a very common application of fishery models, in which a least-squares algorithm is used to estimate population parameters from catch and effort data. For example, a straightforward application of the theory proposed by Schnute (1985) might lead to an analysis similar to example 8. Researchers, faced with such unrealistically low estimates of survival, have sometimes resorted to pure measurement error models to resolve this problem. The combined error structure proposed here appears to be a much better alternative. Remarkably, it leads to estimates of σ and q that are close to those in example 1, where the extra size-frequency data gives the analysis greater certainty. Even with combined error, however, uncertainties in estimation remain. Excluding size-frequency data, it is possible to reject the hypothesis of pure measurement error (example 9) against the hypothesis of combined error (example 7) with 95% confidence, but not the hypothesis of pure process error (example 8).

Examples 10–12 differ from 7–9 only in the estimates of σ and τ. All other estimates and the minimum value of l are identical. This result reflects the effect of the ratio X'/X as a scaling factor in (6.5). The reduction of σ and τ by 11% in examples 10–12, relative to examples 7–9, precisely compensates for the higher value of X'/X in (7.3) and Table 7.

One of our initial aims was to evaluate the Option-2 method of CPUE calculation relative to the 25% method. This is possible by comparing example 13 (Option-2 method) with example 1 (25% method). Estimates of σ, q, τ and λ are essentially identical for the two examples; however, the values of ξ and l are much larger for example 13. Thus, although parameter estimates are apparently unaffected by the method of calculating CPUE, the choice of method has a major effect on parameter variance. The 25% method clearly leads to a better fit.

Our discussion of Table 8 shows that error structure, determined by the parameter λ, greatly influences the resulting parameter estimates. We can assess the importance of λ more generally with a probability profile for λ, calculated by the method described in section 5C. Figure 11 illustrates the outcome for examples 1 and 6. Notice, in particular, that the λ-profile for example 1 crosses the $\lambda = 0$ axis at $p = 0.98$. This feature corresponds precisely to our calculation (8.1) above; thus, the hypothesis $\lambda = 0$ can be rejected with 98% confidence against the alternative $\lambda \neq 0$. The λ-profile for example 6 is

wider than that for example 1, and it crosses the $\lambda = 0$ axis below $p = 0.90$. Both profiles are asymmetric about the minimum and rise steeply as $\lambda \rightarrow 1$. Values of λ as large as those suggested by pure measurement error can be rejected with a high degree of confidence for both examples 1 and 6.

The effect of error structure can also be examined by comparing the residuals δ_t in (5.23) for examples 1–3 (Fig. 12). For example 3 there is an increasing trend in δ_t over the period 1969–86. Thus, pure measurement error could be rejected on the basis of trends in δ_t. There are no obvious trends in δ_t for examples 1 or 2. However, the deviations are smaller and more evenly distributed for the combined error structure (example 1). Note that the extreme δ_t at 1969 is reduced for example 1 relative to example 2. The value δ_1 at 1956 corresponds to an initial residual from (5.23a). Since the (dynamic) model makes no prediction for the first year of data, δ_1 is not calculated directly from the model, but rather extrapolated back from the entire series. In the case of pure process error ($\lambda = 0$), model residuals η_t are uncorrelated, and the future series carries no information about the initial value. Consequently, in this case $\delta_1 = 0$, as illustrated by example 2.

As a further guide to comparing our examples, we examine 95% confidence regions for the parameter pair (σ, q) (Fig. 13), as well as probability profiles for σ (Fig. 14) and q (Fig. 15). The confidence regions for examples 1–4 (Fig. 13A) appear as oblong sections that terminate on the lower limit for q ($q = 0$) and sometimes on the upper limit for σ ($\sigma = 1$). The region for example 3 has a somewhat distinctive shape, but is centered over the regions for examples 1–2. The region for the tag data (example 14) appears elliptical and does not overlap with any of the fishery data regions (examples 1–4).

The intuitive significance of Fig. 13A can be understood by comparison with Fig. 10. Each confidence region in Fig. 13A is centered on a contour (4.11) of constant τ, as suggested by graphical analysis. Specifically, regions in Fig. 13A align with contours in Fig. 10 as follows:

Region (Fig. 13A)	Contour (Fig. 10)
Example 1	$E.\ \tau = 0.78$
Example 2	$E.\ \tau = 0.78$
Example 3	$E.\ \tau = 0.78$
Example 4	$D.\ \tau = 0.60$
Example 14	$A.\ \tau = 0.33$

For examples 1–4, the regions are noticeably bent to follow the contour lines. The elliptical region of example 14 is centered around the estimate (7.6), and bending is not noticeable because the region is confined to a relatively small arc of the contour. This is true particularly because q is rather well determined by (6.9a). Similarly, the regions for examples 1 and 4 do not cover the entire length of the corresponding contour lines because the fishery data contain enough information to define an upper limit for q.

The confidence region for example 1 is narrower than (in fact, completely contained in) the region for example 2. This feature again relates to the utility of a combined error structure. If the extra free parameter λ in example 1 were unimportant, its use would not lead to better definition of the survival parameters. Similarly, the σ-profiles for examples 1 and 2 (Fig. 14A) indicate better definition of σ (narrower confidence intervals for each p-level) with combined error. The q-profiles for examples 1–2 (Fig. 15) are essentially identical.

The confidence region for example 3 (Fig. 13A) forms a narrow band that bulges at the top, along the constraint where $\sigma = 1$. Within this region, there are two local minima of l corresponding to the estimates

(8.2a) $(\hat{\sigma}, \hat{q}) = (0.967, 0.053)$,

(8.2b) $(\hat{\sigma}, \hat{q}) = (0.758, 0)$.

A full contour map for l in example 3 would show these minima rather like lakes on a topographic map. The bulge mentioned above surrounds the "lake" centered at (8.2a). Thus, the process error model is ambiguous. It prefers the estimates (8.2a), which represent the global minimum shown in Table 8; however, it also suggests the alternative estimates (8.2b), which are very close to the estimates in example 1. This ambiguity is especially evident in both the σ-profile (Fig. 14A) and q-profile (Fig. 15) for example 3. The q-profile for this example differs substantially from all others illustrated in Fig. 15.

Confidence regions for examples 1 and 4 do not overlap. The region for example 4 is somewhat broader, as expected by the poorer fit (larger l in Table 8). Evidently, the main effect of altering V' is a shift in the confidence region along the σ-axis. Probability profiles for σ and q confirm this observation. Examples 1 and 4 have similar σ-profiles, but are centered on different values of σ. Except for example 3, q-profiles are largely independent of both V' and error structure.

It is important to remember throughout this discussion that example 1 is the most plausible on the basis of likelihood. The other regions and profiles simply illustrate confusion that would result from other models. Example 3, in particular, implies a false degree of certainty in (σ, q). We do, however, allow for the possibility that V' might be larger than 2.88 kg. Consequently, the confidence region for example 1 might realistically require slight extension to the left, but not upward. Apparently, from examples 1 and 4, an upper confidence limit for q is well defined, independent of V'.

If no size-frequency data are available, then the remaining data provide much less information on σ and q. Confidence regions for examples 7–9 (Fig. 13B) bear little similarity to the corresponding regions for examples 1–3. The regions are bounded by all possible constraints (1.16)–(1.17). Furthermore, the upper boundary of each region appears hyperbolic, with an asymptote along the q-axis. Example 7 gives the broadest of these three regions; this result is at least realistic, as the region includes that obtained in example 1. By contrast, the region for example 8 actually excludes most of the plausible values (σ, q) indicated by example 1. Once again, it appears that pure process error, in the absence of size-frequency data, can be misleading. Interestingly, however, the model with pure measurement error appears to perform better in this case. When $q > 0.7$, the regions for examples 1 and 9 are quite similar.

The σ-profiles for examples 7–10 (Fig. 14B) are much broader than corresponding profiles for examples 1–4. For example, although the estimate for example 7 is similar to that for example 1, the broader profile for example 7 indicates much less confidence in this estimate. The profile for example 8 is somewhat narrower than that for example 7, and, as we might expect by now, leads to a deceptive conclusion. The 95% confidence interval for example 8 excludes the estimate from example 1. The profile for example 9, like that for example 3, shows two minima. There is a global minimum at the estimate ($\sigma = 0.813$) and a local minimum at the lower limit for σ ($\sigma = 0$). The latter accounts for an unusual left limb on the profile.

The absence of size-frequency data appears to have less influence on the estimate of q than it does on the estimate of σ. This is evident in the q-profiles shown in Fig. 15. The profile for example 7 has a similar shape to those for examples 1, 2, and 4, but rises somewhat less steeply. Thus, analysis from example 7 suggests that the fishery has little effect on the stock; however, an upper confidence limit for q is larger than it would be with the use of size-frequency data.

A transformation of the parameters (σ, q) helps explain the strangely shaped confidence regions for examples 7–9. Fig. 16 illustrates confidence regions for the parameter pair (σ, σq) that correspond exactly to the (σ, q)-regions in Fig. 13B. Notice that the equation

$$\sigma q = c,$$

where c is a constant, corresponds to a hyperbola in Fig. 13B and a horizontal line in Fig. 16. Thus, the hyperbolic upper boundaries of regions in Fig. 13B transform to relatively well behaved curves in the (σ, σq)-space of Fig. 16. In particular, the upper boundary for example 7 in Fig. 16 is nearly linear. This relative stability of the parameter σq (as opposed to q) is not surprising, given the model (6.5) used in examples 7–9. Notice that the model's prediction is based on the two terms $(X'/X)I^*_{t-1}$ and $(X'/X)C^*_{t-1}$, where σ and σq are the respective coefficients. In the case of process error ($\lambda = 0$, example 8), the model is nearly linear, and the corresponding confidence region in Fig. 16 has the characteristic elliptical shape associated with linear models. By contrast, the region for example 9 has bulges on the left and right, corresponding to two local minima. This contour, like that for example 3 (Fig. 13A), can be visualized as the result of two "lakes" in the topography of l.

Another significant feature of the parameters chosen in Fig. 16 is that contours of constant survival $\tau = \sigma(1 - qE)$ are linear, rather than hyperbolic as in Fig. 10 and 13. Since the region for example 1 is oriented along a τ-contour, it appears straight in Fig. 16 and bent in Fig. 13. Similarly, the contours for examples 2–4 in Fig. 13A would appear straight if plotted in (σ, σq)-space.

9. Concluding Remarks

It is appropriate at this point to summarize our main conclusions and elaborate on their implications. Also, we must still resolve the discrepancy between parameter estimates obtained from fishery and tag data. In this section, we discuss these issues and comment on areas for further research.

A key feature of our approach is the use of an exact MA(1) error structure. It is well-known (Schnute 1987b, section 2) that different error structures can result in highly different parameter estimates. Typically, information is not available to determine the appropriate error structure. Here, however, the serial nature of the data makes it possible to estimate a parameter λ that resolves this dilemma. By constraining λ to extreme values, we can assess models with pure process error or (approximately) with pure measurement error. Often these extreme models lead to parameter estimates that are misleading, when compared with estimates obtained by analyses that incorporate additional data.

Parameter estimation for the size-structured model involves two dichotomies. First, within the whole population, survival (τ) must be distinguished from recruitment (A^*). Second, survival itself must be divided between natural causes (σ) and fishing ($1 - qE$). Size-frequency data can help resolve the first dichotomy. Resolution of the second depends on evidence that high levels of fishing effort do indeed reduce survival.

In our case, even with available size-frequency data, the dichotomy between survival and recruitment is made somewhat more complex by uncertainty in the growth parameter V'. A higher V' implies a higher recruitment and a correspondingly lower value for survival. Although we used $V' = 3.50$ kg for illustration, we believe that this is an extreme value (Schnute et al. 1989), and that the true value of V' is near 3 kg. The large increase in the model's likelihood (Table 8) for data compiled with $V' = 3.50$ kg compared with $V' = 2.88$ kg supports this conclusion.

Without size-frequency data, it may be difficult to distinguish survival from recruitment, and thus even harder to separate survival into components associated with natural causes and fishing. This point is clearly illustrated by the (σ, q)-contour for example 7 in Fig. 13B. The value of σ spans the entire admissible range ($0 \leq \sigma \leq 1$). Even with size-frequency data, the distinction between natural and fishing mortality may be unclear, if there is insufficient contrast in the effort time series. Our analysis (example 1) indicates that the fishery is having little, if any, effect on the lingcod stock. The effort data do, however, provide enough contrast to define an upper 95% confidence limit for q at about $0.045 \times 10^{-3}\,\mathrm{h}^{-1}$ (Fig. 15), regardless of the value of V'. Based on a typical effort $E = 3.88 \times 10^3$ h (Table 7), this suggests that survival from fishing ($1 - qE$) is typically at least as high as 83%. A corresponding 95% confidence interval for σ (Fig. 14A) is 0.70–0.93 if $V' = 2.88$ kg (or 0.50–0.73 if $V' = 3.50$ kg).

We have shown that a higher estimate of V' is associated with greater total mortality and unchanged fishing mortality. Thus, the higher our estimate of V', the smaller the proportion of total mortality accounted for by fishing. Since we have chosen the relatively small value $V' = 2.88$ kg, our analysis errs by tending to overestimate the effect of the fishery. Of course, the estimate of V' is dependent on the choice of V. Although we believe the value $V = 2.25$ kg to be the most appropriate choice for the lingcod example (Schnute et al. 1989, section 3B), we have repeated the entire analysis with $V = 2.75$ kg. This is the left end point of the size interval centered on 3.00 kg, illustrated in figure 1 of our companion paper (Schnute et al. 1989). The corresponding estimate of V' from tag data turns out to be $V' = 3.39$ kg. An analysis based on these values of V and V' leads to essentially the same conclusions presented here. In fact, parameter estimates from this analysis agree to two or three decimal places with comparable estimates in Table 8.

One of our initial aims was to compare results obtained from different indices of abundance, and we used two methods to calculate CPUE. A researcher may favor one such index over another if it appears to encompass greater biological reality. The Option-2 method, for example, accounts for the depth distribution of the fish stock. We found a large difference in the corresponding values of l for the two methods, and the 25% method clearly leads to a better fit. The 25% method also has the advantage that it is easier to compute. This is one case in which the collection of extra information from the fishery (i.e. depth of trawl) appears not to be justified by a reduction in model variance.

One potential difficulty with our entire analysis is that the fishery and tag data lead to fundamentally different estimates of the parameters (σ, q, τ). Explicitly, we obtain

$$(9.1)\quad (\hat{\sigma}, \hat{q}, \hat{\tau}) = (0.760,\ 0.000 \times 10^{-3}\,\mathrm{h}^{-1},\ 0.760)$$

from the fishery data (Table 8, example 1) and

$$(9.2) \quad (\hat{\sigma}, \hat{q}, \hat{\tau}) = (0.455, 0.071 \times 10^{-3}\,\mathrm{h}^{-1}, 0.326)$$

from the tag data (Table 8, example 14). Furthermore, Fig. 13A indicates that the difference between (9.1) and (9.2) is real statistically. Since a separate analysis, based on an equilibrium model for the size-frequency data, gives (Table 5)

$$(9.3) \quad \hat{\tau} = 0.78,$$

(9.1) is certainly more credible than (9.2). If survival really were as small as that indicated in (9.2), it would be impossible to account for the significant number of large (old) fish observed in the population.

One possible explanation for (9.2) might focus on common sources of error in a tag–recovery experiment. These include (i) mortality due to tagging, (ii) tag loss, (iii) nonreporting of tags, and (iv) nonrandom mixing of tagged fish within the total population. The first three sources represent tagged fish that are effectively lost to the experiment. If these fish had died from natural causes, the consequence to the analysis would have been equivalent. Thus, the disappearance of these fish is counted as natural mortality, resulting in underestimates of σ and τ. We believe, however, that (i)–(iii) are unlikely to account completely for the large discrepancy between (9.1) and (9.2).

The fourth explanation, nonrandom mixing of tagged fish within the total population, is probably closer to the truth in this case. Our reasons for making this claim depend on circumstances particular to the fishery. Traditional trawl grounds cover only a minor proportion of Area 3C–N. Large boulders make trawling hazardous in some sections (Luternauer et al. 1986). Lingcod probably prefer these rocky areas, so that only a small component of the population may be available to the fishery. Furthermore, when fish are removed from trawlable grounds, others from nearby rocky areas may move into the newly vacated habitat. It may also happen that survivors from the fishery move slowly out to rocky areas when space becomes available there. Thus, fish may mix slowly between trawlable and nontrawlable habitats.

Under the above "slow-mixing" scenario, data from the fishery reflect the whole underlying population in both habitats. For example, if a large catch is taken from the trawl grounds one year, the fish may be replaced in the next year by emigrants from rocky areas. The fishery model would thus detect the high survival and low catchability indicated in (9.1). By contrast, if mixing is slow, tagged fish that linger on the trawl grounds would be exposed to higher fishing mortality than the general population (which resides largely in rocky areas). Thus, the higher value of q in (9.2) may reflect catchability relative to the trawlable areas only. Finally, as tagged survivors slowly leave the trawl grounds for rocky regions, the tag model explains their absence as natural mortality, giving the low value of σ in (9.2).

The interpretive analysis presented in this section illustrates the broad utility of the methods here. Since the underlying model has a biological basis, we can compare results from various data sets and analyses, such as (9.1)–(9.3), to devise specific scenarios consistent with the full set of available information. Furthermore, the model's statistical component allows us to temper our logic with an honest sense of what we do not know. For example, from Fig. 13A, we are prepared to believe that the difference between (9.1) and (9.2) is real, although we know that the parameters σ and q are confounded somewhat. We even have intuitive faith in these conclusions, because we anticipated them from simple arguments suggested by graphical analysis.

We recognize that, in spite of our lengthy analysis, we have failed to address several points of legitimate concern. Some of these apply specifically to the lingcod example, and others apply more generally to the model itself. For the lingcod example, we can cite at least three areas where further investigation is warranted: (1) the apparent intervention in ω^* and A^* near 1969, (2) environmental interactions, and (3) multi-species effects. Several hypotheses might be examined to account for the intervention (1), including changes in catchability, the sex ratio of the catch, or growth rates. All such changes could alter the newly recruited weight interval (V, V'). Environmental interactions (2) could be investigated by relating model residuals to various environmental time series. Similarly, since lingcod are caught as part of a multi-species fishery, multi-species effects (3) could be examined by relating residuals to abundance indices for other species.

Apart from the specifics of the lingcod example, we note at least two areas where more detailed investigation of the statistical model is warranted: (i) sensitivity to deviations from model hypotheses and (ii) design of management policies. In principle, simulation could be used to test (i), the model's sensitivity to deviations from the hypotheses. This is difficult to do convincingly, however, because such deviations might occur in an infinite variety of ways. For example, results from a closed population model might be irrelevant if, in reality, there is a refuge area from the fishery.

We have not even addressed the complex topic (ii), the design of management policies. Although this was not critical in our example, where the fishery currently appears to have a minor effect on the stock, most fishery models are designed primarily as tools for policy development. Again, however, we are faced with the fact that even the most sophisticated management models, based on extensive simulation studies, may fail if the underlying model itself is inadequate or wrong.

We believe that our approach represents a legitimate first step in fish stock analysis. The methods are simple and flexible enough to investigate the validity of the model itself, as in our discussion of a possible refuge area. Because of uncertainty in fishery data, intuition must necessarily play an important role in formulating management policy. Even a brilliantly designed model can be misleading if it misrepresents major features of the stock. We prefer simply to construct coherent arguments that honestly acknowledge uncertainty in both data and model hypotheses.

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Appendix A. Equilibrium Distribution

The model described in the body of this paper uses t as a discrete variable with integer values. Consider, for example, a group of newly recruited fish with weight V at time $t = 0$. If $w(t)$ denotes the weight of each fish at a later time t, then it can be proved inductively from (1.6) and (1.12) that (when $\rho \neq 1$)

$$w(t) = V + (V' - V)\cdot\frac{1 - \rho^t}{1 - \rho}, \tag{A.1}$$

where, in particular, $w(0) = V$ and $w(1) = V'$.

The weight $w(t)$ in (A.1) is, in fact, a particular case of Schnute's (1981, equation (15)) general growth law with the following substitutions: $y_1 = V$, $y_2 = V'$, $\tau_1 = 0$, $\tau_2 = 1$, $e^{-a} = \rho$, and $b = 1$. Thus, (A.1) is valid for real values $t \geq 0$, if we asume von Bertalanffy growth ($b = 1$ in Schnute 1981) during time intervals between integer values of t. This is a reasonable extension of the Ford–Walford growth law (1.6), which is often derived from von Bertalanffy growth (Ricker 1975, p. 222). Notice that, in the present context, t represents the time since a fish had weight V. Fish with the same weights may have different ages, but the weight $w(t)$ is determined by the time t since a fish reached weight V. In fact, the function $w(t)$ defines a one-to-one map between time t and weight w. For a given w, the corresponding value of t is

$$t = \ln\left[\frac{(V' - w) - \rho(V - w)}{V' - V}\right]/\ln(\rho). \tag{A.2}$$

The concept of survival can similarly be extended to real, rather than integer, time intervals. Thus, after 1 yr the survival fraction is τ, after two years it is τ^2, and so on. In general, the survival fraction $\tau(t)$ after t years is

$$\tau(t) = \tau^t. \tag{A.3}$$

Like (A.1), (A.3) has an obvious extension to real $t \geq 0$. In this case, we make the usual assumption (Ricker 1975, p. 8) that mortality follows an exponential decay law. Thus, if Z is the instantaneous mortality rate, then $\tau(t) = e^{-Zt}$ and $\tau = e^{-Z}$.

Based on the above descriptions of mortality and growth, we can now extend (4.1) to continuous time. In this case, the assumption is that

$$\int_{w(t_2+t)}^{w(t_2+t)} N(w)\,dw = \tau^t \int_{w(t_1)}^{w(t_2)} N(w)\,dw, \tag{A.4}$$

for arbitrary positive numbers t_1, t_2, and t with $t_1 < t_2$. We can relate (A.4) to (4.1) by noting that times t_1 and t_2 correspond to weights $w_1 = w(t_1)$ and $w_2 = w(t_2)$. Furthermore, $w_i' = w(t_i + 1)$ for $i = 1, 2$. Thus (A.4) is identical to (4.1) when $t = 1$. More generally, within an arbitrary weight interval (w_1, w_2), (A.4) describes the combined effect of growth and survival after an arbitrary time $t > 0$.

To convert (A.4) to differential form, divide both sides by $t_2 - t_1$ and let t_2 tend to t_1. This gives

$$Dw(t_1 + t)\cdot N[w(t_1 + t)] = \tau^t \cdot Dw(t_1)\cdot N[w(t_1)], \tag{A.5}$$

where Dw represents the derivative dw/dt. Specifically, from (A.1), this derivative is

$$Dw = -\rho^t\cdot\ln(\rho)\cdot\frac{V' - V}{1 - \rho}. \tag{A.6}$$

Furthermore, combining (A.5)–(A.6) and setting $t_1 = 0$ gives

$$N[w(t)] = (\tau/\rho)^t \cdot N_v, \tag{A.7}$$

where $N_V = N(V)$. This result has biological meaning, since a fish starting at weight V will grow to weight $w(t)$ after time t. The factor $(\tau/\rho)^t$ in (A.7) accounts for the change in population density due to survival and growth during this time.

The result (4.2) is essentially a transformation of (A.7). The idea is to use the inverse function (A.2) to express t in terms of w. The left side of (A.7) then reduces simply to $N(w)$. On the right side, it can be shown from (A.2) that

$$(\tau/\rho)^t = \left[\frac{(V' - w) - \rho(V - w)}{V' - V}\right]^{\ln(\tau/\rho)/\ln(\rho)} \tag{A.8}$$

Combining (A.7) and (A.8) proves (4.2).

The remaining proofs required for section 4 are straightforward from (4.2). Thus, computing the integral

$$N = \int_V^{W_\infty} N(w)\,dw$$

from (4.2) gives (4.3), where the definition (1.13) of W_∞ leads to slightly different calculations when $\rho < 1$ or $\rho > 1$. Furthermore, the distribution

$$\theta(w) = N(w)/N$$

in (4.4) follows at once by dividing (4.2) by (4.3). Finally, the cumulative distribution $\Theta(w)$ is the integral of (4.4). Although these calculations are somewhat tedious, they can be accomplished routinely with the aid of a table of integrals (or a good memory of integral calculus).

The above arguments, starting with (A.1), consistently assume that $\rho \neq 1$. In all cases, however, they can be extended to the case $\rho = 1$ by taking limits as ρ tends to 1. In particular, (4.7) and (4.8) follow from such considerations.

It remains only to prove (4.9)–(4.10). Since

$$(V' - w') - \rho(V - w') = \rho[(V' - w) - \rho(V - w)],$$

it follows from (4.5) that

$$\frac{1 - \Theta(w')}{1 - \Theta(w)} = \rho^{\log(\tau)/\log(\rho)} = \tau.$$

This implies (4.10); furthermore, since $dw'/dw = \rho$, differentiating (4.10) with respect to w gives (4.9). This completes the proof of all results in section 4.

Appendix B. Exact Likelihood for Model (5.18)

This appendix derives the exact likelihood function (5.25) for model (5.18). In most of this derivation, the model parameters Φ, λ, and ξ are assumed to have prescribed (fixed) values, and we suppress reference to them where possible without confusion. The data Q_T, $t = 1,\ldots,T$, are presumed known, although the likelihood function relates only to statistical variation in $Q_{K+1},\ldots,Q_T$. The initial observations $Q_1,\ldots,Q_K$ are assumed independent of model parameters.

The model itself can be defined by two equations:

(B.1a) $\eta_t = Q_t - H(Q_{t-1},\ldots,Q_{t-K})$,

(B.1b) $\delta_t = \eta_t + \lambda\delta_{t-1}$.

These are equivalent to (5.18) if

(B.2) $\delta_t = \xi\epsilon_t$.

Define the three vectors:

$$\mathbf{Q} = (Q_{K+1},\ldots,Q_T),$$

$$\boldsymbol{\eta} = (\eta_{K+1},\ldots,\eta_T),$$

$$\boldsymbol{\delta} = (\delta_{K+1},\ldots,\delta_T).$$

Notice that (B.1a) defines $\boldsymbol{\eta}$ from $\mathbf{Q}$, and, if δ_K is known, then (B.1b) defines $\boldsymbol{\delta}$ iteratively from $\boldsymbol{\eta}$. The matrix of derivatives

$$\left(\left(\frac{\partial\eta_t}{\partial Q_s}\right)\right)_{s,t=K+1}^{T}$$

is triangular with the entry "1" along the main diagonal, so that the Jacobian $\partial\boldsymbol{\eta}/\partial\mathbf{Q}$ of this matrix is 1. Similarly, the Jacobian $\partial\boldsymbol{\delta}/\partial\boldsymbol{\eta}$ is also 1.

For given values of the model parameters, the vector $\boldsymbol{\eta}$ is simply a transformed version of the data vector $\mathbf{Q}$. Consequently,

(B.3) $L(\mathbf{Q}) = L(\boldsymbol{\eta})\,\partial\boldsymbol{\eta}/\partial\mathbf{Q}$,

where $L(\cdot)$ denotes the likelihood of the indicated vector. Similarly, given δ_K, $\boldsymbol{\delta}$ is equivalent to $\boldsymbol{\eta}$, and

(B.4) $L(\boldsymbol{\eta}, \delta_K) = L(\boldsymbol{\delta}, \delta_K)\,\partial\boldsymbol{\delta}/\partial\boldsymbol{\eta}$.

Since the unconditional likelihood $L(\boldsymbol{\eta})$ is the integral

(B.5) $L(\boldsymbol{\eta}) = \int_{-\infty}^{\infty} L(\boldsymbol{\eta}, \delta_K)\,d\delta_k$,

it follows from (B.3)–(B.5) that

(B.6) $L(\mathbf{Q}) = \int_{-\infty}^{\infty} L(\boldsymbol{\delta}, \delta_K)\,d\delta_k$,

where we have used the fact that the Jacobians in (B.3)–(B.4) are 1. The integral (B.6) expresses the desired likelihood $L(\mathbf{Q})$ in terms of a particularly simple likelihood, since, by (B.2), the variates δ_t are independent and normal with mean 0 and variance ξ^2. Thus, the likelihood $L(\boldsymbol{\delta}, \delta_K)$ is the usual product of normal distributions:

$$\text{(B.7)}\quad L(\boldsymbol{\delta}, \delta_K) = \left(\frac{1}{\sqrt{2\pi}\,\xi}\right)^{T-K+1} \exp\left[-\frac{1}{2\xi^2}\sum_{t=K}^{T}\delta_t^2\right].$$

From (B.1b), it can be proved iteratively that

$$\text{(B.8)}\quad \delta_t = \lambda^{t-K}\delta_K + \sum_{s=1}^{t-K}\lambda^{t-K-s}\eta_{K+s},$$

for $t = K + 1,\ldots,T$. By the definition (5.21) of ζ_t, (B.8) can also be written in the simpler form

$$\text{(B.9)}\quad \delta_t = \zeta_t + \lambda^{t-K}\delta_K,$$

for $t = K,\ldots,T$, since $\zeta_K = 0$. Consequently, the sum of squares

$$\text{(B.10a)}\quad S_1 = \sum_{t=K}^{T}\delta_t^2$$

that appears in (B.7) can be written as

$$\text{(B.10b)}\quad S_1 = \sum_{t=K}^{T}(\zeta_t + \lambda^{t-K}\delta_K)^2.$$

It is possible to partition the sum of squares S_1 into two components, one that involves only the series ζ_t and another that involves only δ_K. To accomplish this, solve the equation

$$\partial S_1/\partial\delta_K = 0$$

for δ_K to obtain the value

$$\text{(B.11)}\quad \hat{\delta}_K = -\frac{\sum_{t=K}^{T}\lambda^{t-K}\zeta_t}{\sum_{t=K}^{T}\lambda^{2(t-K)}}$$

that minimizes S_1. Since the geometric series in the denominator above sums to $D(\lambda)$ in (5.20), the expression (B.11) for $\hat{\delta}_K$ is the same as that for δ_K in (5.23a). Furthermore, a short calculation shows that

$$\text{(B.12)}\quad \partial^2 S_1/(\partial\delta_K)^2 = 2D(\lambda).$$

Since S_1 is a quadratic function of δ_K, the Taylor expansion of S_1 at $\hat{\delta}_K$ is exact:

$$\text{(B.13)}\quad S_1 = \sum_{t=K}^{T}(\zeta_t + \lambda^{t-K}\hat{\delta}_K)^2 + D(\lambda)\,(\delta_K - \hat{\delta}_K)^2,$$

where the first order term in $\delta_K - \hat{\delta}_K$ is absent because $\partial S_1/\partial\delta_K = 0$ at $\hat{\delta}_K$ and the coefficient of the second order term comes from (B.12). Using the notation of (5.23)–(5.24), (B.13) reduces to

$$S_1 = S(\Phi, \lambda) + D(\lambda)\,(\delta_K - \hat{\delta}_K)^2. \tag{B.14}$$

This is the desired partition of the sum of squares S_1.

Combining (B.7), (B.10), and (B.14) gives

$$L(\boldsymbol{\delta}, \delta_K) = \left(\frac{1}{\sqrt{2\pi}\,\xi}\right)^{T-K} \exp\left[-\frac{S}{2\xi^2}\right] \times \left(\frac{1}{\sqrt{2\pi}\,\xi}\right) \exp\left[-\frac{D}{2\xi^2}(\delta_K - \hat{\delta}_K)^2\right]. \tag{B.15}$$

From (B.6), the desired likelihood $L(\mathbf{Q})$ can be obtained by integrating δ_K out of (B.15):

$$L(\mathbf{Q}) = \left(\frac{1}{\sqrt{2\pi}\,\xi}\right)^{T-K} \frac{1}{\sqrt{D}} \exp\left[-\frac{S}{2\xi^2}\right], \tag{B.16}$$

since the integral of the second factor on the right side of (B.15) is $D^{-1/2}$.

To complete the proof, define

$$l_1 = -2\cdot\log[L(\mathbf{Q})],$$

which, from (B.16) is

$$l_1 = (T-K)\cdot\log(2\pi\xi^2) + \log(D) + \xi^{-2}S. \tag{B.17}$$

Solving the equation $\partial l_1/\partial\xi = 0$ for ξ gives the maximum likelihood estimate

$$\hat{\xi} = [S/(T-K)]^{1/2}. \tag{B.18}$$

Substituting (B.18) into (B.17) gives

$$l_1(\hat{\xi}) = \log(D) + (T-K)\cdot\log(S) + (T-K)\cdot\log[2\pi e/(T-K)],$$

and this is the same as $l(\Phi, \lambda)$ in (5.25), except for a constant.

Appendix C. Measurement and Process Error Variances

In this appendix we derive expressions for measurement and process error variances associated with models in section 6. The arguments are analogous to those developed in (5.13)–(5.16), except that approximations are required to deal with square root transformations. For example, the model

$$(J_t^*)^{1/2} = [\sigma v_{t-1}(J_{t-1}^* - qC_{t-1}^*)]^{1/2} + \phi\epsilon_t, \tag{C.1a}$$

$$(I_t^*)^{1/2} = (J_t^*)^{1/2} + \psi\delta_t, \tag{C.1b}$$

is a counterpart of (6.1) with process and measurement error variances ϕ^2 and ψ^2, respectively. Here, as in (5.8), J_t^* represents a true value for I_t^*, without measurement error.

If we assume that ψ is small in (C.1b), then it follows that

$$(J_t^* - qC_t^*)^{1/2} = \{[(I_t^*)^{1/2} - \psi\delta_t]^2 - qC_t^*\}^{1/2} \tag{C.2a}$$

$$\simeq (I_t^* - qC_t^*)^{1/2} - \left(\frac{I_t^*}{I_t^* - qC_t^*}\right)^{1/2}\cdot\psi\delta_t \tag{C.2b}$$

$$= (I_t^* - qC_t^*)^{1/2} - (1 - qE_t)^{-1/2}\cdot\psi\delta_t, \tag{C.2c}$$

where the approximation in (C.2b) represents a Taylor expansion of order 1 in ψ. It follows that (C.1) is approximately equivalent to the model

$$(I_t^*)^{1/2} = [\sigma v_{t-1}(I_{t-1}^* - qC_{t-1}^*)]^{1/2} + \eta_t, \tag{C.3a}$$

$$\eta_t = \phi\epsilon_t + \psi\delta_t - \left(\frac{\sigma v_{t-1}}{1 - qE_{t-1}}\right)^{1/2}\cdot\psi\delta_{t-1}. \tag{C.3b}$$

If v and E are typical values of v_t and E_t, respectively, then it follows from (C.3b) that the covariance matrix of η_t is approximately

$$\mathrm{Var}[\eta_t] = \phi^2 + \psi^2(1 + \zeta^2), \tag{C.4a}$$

$$\mathrm{Cov}[\eta_t, \eta_{t-1}] = -\psi^2\zeta, \tag{C.4b}$$

where ζ is given by (6.2). Furthermore, comparing (C.3) and (6.1) shows that the models are similar, except that the error

$$\eta_t = \xi(\epsilon_t - \lambda\epsilon_{t-1})$$

in (6.1) has covariance matrix (5.13). Thus, (C.4) and (5.13) imply the equations

$$\phi^2 + \psi^2(1 + \zeta^2) = \xi^2(1 + \lambda^2), \tag{C.5a}$$

$$\psi^2\zeta = \xi^2\lambda. \tag{C.5b}$$

Solving (C.5) for ϕ^2 and ψ^2 gives (6.3).

Analogous to (C.1), a counterpart of (6.5) with measurement and process error is

$$(J_t^*)^{1/2} = [A^* + \sigma(X'/X)\,(J_{t-1}^* - qC_{t-1}^*)]^{1/2} + \phi\epsilon_t, \tag{C.6a}$$

$$(I_t^*)^{1/2} = (J_t^*)^{1/2} + \psi\delta_t. \tag{C.6b}$$

An approximation to (C.6) for small ψ, similar to the earlier approximation (C.3), is

$$(I_t^*)^{1/2} = [A^* + \sigma(X'/X)\,(I_{t-1}^* - qC_{t-1}^*)]^{1/2} + \eta_t, \tag{C.7a}$$

$$\eta = \phi\epsilon_t + \psi\delta_t - \frac{\sigma(X'/X)}{[(A^*/I_{t-1}^*) + \sigma(X'/X)\,(1 - qE_{t-1})]^{1/2}}\cdot\psi\delta_{t-1}. \tag{C.7b}$$

If I^* and E are typical values of I_t^* and E_t, respectively, then an approximate covariance matrix of η_t in (C.7) turns out to be (C.4), where in this case ζ is given by (6.6). Comparing this matrix with the corresponding error matrix for (6.5) again leads to (C.5). Solving (C.5) for ϕ^2 and ψ^2 now gives (6.7), an approximate expression for measurement and process error variances in model (6.5).

Recent Changes in the Phytoplankton of the Bay of Quinte, Lake Ontario: the Relative Importance of Fish, Nutrients, and Other Factors

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A 50% reduction in phosphorus loading to the upper Bay of Quinte (Lake Ontario) from municipal sources in 1977 was followed by a major decline in phytoplankton biomass in 1978. However, by 1984–85, biomasses again approached those of the pre-phosphorus control period, despite continued low phosphorus loadings. No major shifts in phytoplankton composition occurred; domination by the diatoms *Melosira* and *Stephanodiscus* spp. and the blue-green algae *Anabaena* and *Aphanizomenon* spp. has continued. Highly significant positive correlation coefficients (r = 0.92–0.98) were found for phytoplankton — fish relationships during both the pre- and postphosphorus removal periods which coincided with pre- and postdie-off periods of white perch (*Morone americana*) and alewife (*Alosa pseudoharengus*). For the entire 16-yr period of data collection, a multiple regression model fitting upper bay phytoplankton biomass (with an adjusted R^2 of 0.83) was developed with five input variables. White perch biomass alone explained more than 50% of the variance in the model. It is hypothesized that trophic interactions among other biotic components in the Bay of Quinte may be very important in controlling phytoplankton biomass.

La diminution de 50 % de la charge en phosphore d'origine urbaine, survenue en 1977 dans la partie supérieure de la baie de Quinte (lac Ontario), a été suivie d'une diminution importante de la biomasse phytoplanctonique en 1978. Cependant, vers 1984–85, les biomasses étaient encore voisines de celles de la période précédant la limitation des concentrations de phosphore, même si les charges en phosphore restaient toujours faibles. Aucune modification importante de la composition du phytoplancton n'est survenue; la domination des diatomées *Melosira* et *Stephanodiscus* spp. et des cyanophycées *Anabaena* et *Aphanizomenon* spp. s'est poursuivie. On a trouvé des coefficients de corrélation positive hautement significatifs (r = 0,92–0,98) dans le cas des relations phytoplancton-poisson durant les deux périodes précédant et suivant l'élimination du phosphore, périodes qui coïncidaient avec les périodes précédant et suivant la mortalité massive de bars-perches (*Morone americana*) et de gaspareus (*Alosa pseudoharengus*). Pour la totalité de la période de 16 ans durant laquelle on a recueilli des données, on a élaboré un modèle de régression multiple adapté à la biomasse du phytoplancton de la baie supérieure (avec un R^2 ajusté de 0,83) en utilisant cinq variables d'entrée. La biomasse représentée par les bars-perches a expliqué plus de 50 % de la variance du modèle. On suppose que les interactions trophiques qui existent parmi d'autres composants biotiques de la baie Quinte peuvent jouer un rôle très important dans le contrôle de la biomasse phytoplanctonique.

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The Bay of Quinte of Lake Ontario was subjected to many decades of excessive phosphorus loadings that resulted in a highly eutrophic condition characterized by high phytoplankton biomass including frequent blue-green algal blooms (Johnson and Owen 1971; Johnson 1986). Other components of the bay ecosystem also exhibited signs of severe degradation. The areal extent of aquatic macrophyte growth was reduced in large part because of shading from high phytoplankton concentrations (Crowder and Bristow 1986). Fish populations were dominated by small-bodied planktivores and benthivores such as alewife (*Alosa pseudoharengus*) and the recent invader, white perch (*Morone americana*), while larger centrarchids, lake whitefish (*Coregonus clupeaformis*), lake herring (*Coregonus artedii*), and walleye (*Stizostedion vitreum*) were reduced to remnant populations (Hurley and Christie 1977; Hurley 1986a).

Rehabilitation of the bay ecosystem was based on the control of phosphorus inputs from municipal sewage treatment plants. Field programs that documented the condition of various abiotic and biotic components of the bay were initiated in 1972 under the title of "Project Quinte"[1]. This was a multi-agency, multi-

[1]The findings of Project Quinte spanning the period of scientific investigations from 1972 to the early 1980's were recently published as "Project Quinte: Point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario", Minns, C. K., D. A. Hurley, and K. H. Nicholls [ed.] Can. Spec. Publ. Fish Aquat. Sci. 86: 270 p.

year investigation of the Bay of Quinte ecosystem in which conditions prior to and following after the implementation of phosphorus loading controls were measured and compared.

Among the changes that were recorded when phosphorus removal became effective was a 50% reduction in the mean May–October phytoplankton biomass in the upper Bay of Quinte (Nicholls et al. 1986). However, the same taxa that typified the earlier eutrophic conditions, *Anabaena, Aphanizomenon, Melosira*, and *Stephanodiscus* spp., continued to dominate the phytoplankton community.

There were significant changes in the fish community that occurred at this time, but these were related more to climate anomolies (record cold winters in 1976–77 and 1977–78) than to phosphorus control programs. There was a dramatic crash of both alewife and white perch populations in the bay and an equally dramatic resurgence of walleye year classes in 1977 and particularly in 1978 (Hurley 1986a, Ridgway et al. 1989).

While the initial (1978–81) decrease in phytoplankton biomass fitted the nutrient effect hypothesis (Nicholls et al. 1986), later results showed that phytoplankton biomass increased again in spite of continued low phosphorus loadings. This increase led to an examination of the role of variables such as water temperature, river flows, lake levels, and planktivorous and benthivorous fish biomass in explaining changes in phytoplankton biomass.

Food web interactions have recently been cited as a major influence on biomass at other trophic levels (see review by Northcote 1988). The purpose of this paper is to examine the whole series of phytoplankton and fish data from 1972 to 1987 to explain the relative roles of nutrients, abiotic, and biotic factors on phytoplankton biomass.

Methods

The methods of sample collection and analyses of nutrients, phytoplankton and other variables reported in this paper were as outlined by Robinson (1986) and Nicholls et al. (1986). Sampling locations are also unchanged. However, after 1982, fewer sampling stations were included in the limnological monitoring and the sampling frequency was reduced to bi-weekly. Only data from the upper and middle bay (stations B and HB) are presented here. Average May–October phytoplankton composition and biomass have been determined on pooled samples (Nicholls et al. 1986). Analyses of all samples collected approximately weekly from the Belleville water supply intake have continued. The term "biomass" has been used to describe phytoplankton density in this paper; measurements have been made as biovolume (cubic millimetres) for Project Quinte sampling stations which was equated to biomass on the assumption that the specific gravity of phytoplankton equals 1.0. Phytoplankton samples collected from the Belleville water treatment plant intake were analyzed independently and quantitatively expressed as Areal Standard Units (A.S.U.) (Nicholls et al. 1986).

Fish sampling was as described in Hurley (1986a). In particular, monthly bottom trawls were used in the upper bay to provide population estimates of the major fish species for the multiple regression analyses reported in this paper. Data were expressed as geometric mean biomass over the monthly June to September sampling periods, except in 1982 when trawling was done in September only.

Point-source phosphorus loads from sewage treatment plants discharging to the upper bay were calculated according to Minns et al. (1986) and for recent years were provided by G. Owen (Ministry of the Environment, Kingston, Ont., Canada). May to October average loads for 1972–77 were not available but were estimated from the average ratio of annual loads to May–October loads for the 1978–86 period. Flow data for the Trent River, which drains 80% of the land area above the upper bay and is therefore a useful index of total water input to the upper bay, were obtained for the Glen Ross gauging station from Environment Canada. Lake Ontario water level data were obtained from the U.S. Army Corps of Engineers (Monthly Bulletin of Lake Levels for the Great Lakes). Water temperature data for the upper bay were available in the daily records of the Belleville water treatment plant (Belleville Utilities Commission, 2 Sydney St., Belleville, Ont.).

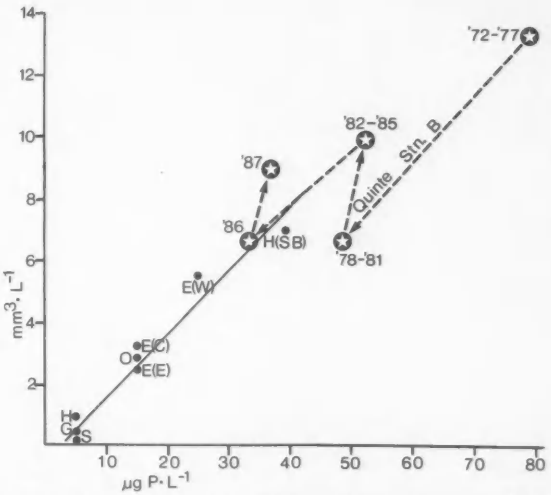

FIG. 1. Changes in May–October phytoplankton biomass ($mm^3 \cdot L^{-1}$) and total phosphorus concentrations ($\mu g\ P \cdot L^{-1}$) at station B in the upper Bay of Quinte 1972–87. Also shown are average values for other Great Lakes locations, keyed as follows: H(SB) = Saginaw Bay of Lake Huron; E(W), E(C), and E(E) = Lake Erie, western, central, and eastern basins, respectively; O = Lake Ontario; H = Lake Huron; G = Georgian Bay; S = Lake Superior. Data sources include Bierman and Dolan (1981), Munawar and Munawar (1981), and Weiler (1981).

Statistical analyses included principal components analysis, simple and multiple linear regression of phytoplankton biomass as the dependent variable with up to 15 independent variables. These variables included the biomass of several fish species, mean monthly water temperatures (May–September), mean monthly water levels, mean monthly Trent River flows, point-source phosphorus loads from sewage treatment plants discharging into the bay, and mean total phosphorus and total nitrogen concentrations for the May–October period at station B in the upper Bay of Quinte.

Principal components analysis was performed on the correlation matrix of independent variables. Both the scree test and eigenvalues greater than 1.0 were used as criteria for significance (Cattell 1978; Draper and Smith 1981).

Multiple linear regressions were calculated from suitably transformed variables, in the case of the principal components, or from untransformed data as in the case of the recorded temperatures, nutrients, and fish biomasses. Both an all subset regression where all variables are examined and stepwise regression where variables are entered and removed as they sig-

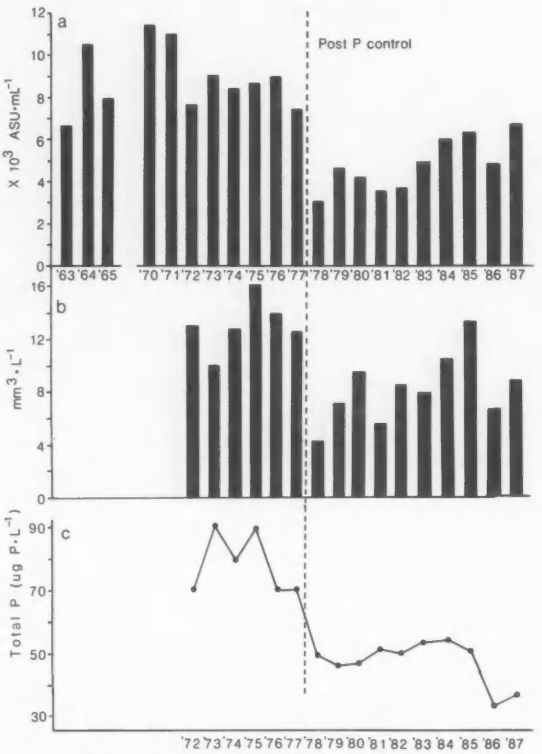

FIG. 2. Average May–October densities of total phytoplankton in samples collected (a) through the Belleville water treatment plant intake and (b) at station B in the upper Bay of Quinte. Also shown (c) are average total phosphorus concentrations over the same time period at station B.

TABLE 1. Inputs of total phosphorus from wastewater treatment plants discharging to the upper Bay of Quinte (Trenton, CFB-Trenton, Belleville)[a]. Estimates are made for the entire year (annual) and for the May–October period only.

Year	Annual (kg P·d^{-1})	May–October (kg P·d^{-1})
1972–75	126	98[b]
1976	90	70[b]
1977	77	60[b]
1978	42	40
1979	32	22
1980	39	29
1981	47	44
1982	44	39
1983	43	26
1984	52	45
1985	29	20
1986	32	30
1987	25	23

[a]Data supplied by G. Owen, Ontario Ministry of the Environment for the 1986 Project Quinte Annual Report.

[b]Estimated from average ratio of annual to May–October inputs 1978–86.

nificantly enter the regression were used. Criteria for significance were generally 't' values that resulted in $P < 0.05$, Mallows' Cp statistic that equals the number of parameters plus the intercept in the model (Draper and Smith 1981), and a high value for the adjusted R^2.

Results

During the early postphosphorus control period of 1978–81, the May–October average phytoplankton biomass was reduced to 50% of the pre-phosphorus control period average of 13.1 mm^3·L^{-1} measured during 1972–77 in the upper Bay of Quinte (Fig. 1). The yield of phytoplankton per unit total phosphorus during both periods was significantly lower than that predicted from phytoplankton and phosphorus data from other areas of the Great Lakes (Fig. 1). More recently (1982–85), there was a well defined trend to much higher phytoplankton biomass in the upper bay, both in samples from the Belleville water intake and from Project Quinte station B (Fig. 2). The 1985 May–October average of 13.3 mm^3·L^{-1} at station B is comparable with values recorded during the prephosphorus control period of 1972–77. These recent increases in the upper bay were also substantiated by elevated chlorophyll *a* concentrations and vertical light extinction coefficients (E.S. Millard, Department of Fisheries and Oceans, CCIW, Burlington, unpubl. data). In contrast, May–October total phosphorus concentrations at station B changed little between 1978 and 1985 (Fig. 1, 2).

Phytoplankton biomass declined dramatically in 1986 (6.7 mm^3·L^{-1}), as did average total phosphorus concentration in the upper bay (33 μg P·L^{-1}). Increases of 34 and 12% in average phytoplankton biomass and average total phosphorus, respectively, were observed in 1987. Point-source phosphorus loadings were substantially lower after 1977 and for the May–October periods were the lowest on record in 1985 (Table 1).

No dramatic changes have occurred in the phytoplankton composition of the upper bay. Although the Dinophyceae were only a minor component of the upper bay phytoplankton during the earlier years of the study (averaging 4% of the total during 1972–77), this group has declined in importance in recent years to a level similar to that contributed by the Chrysophyceae (about 1% of the total phytoplankton; Table 2). Bacillariophyceae (diatoms) and Cyanophyceae (blue-green algae) have continued to dominate the May–October periods. Total diatom biomass has generally been about 2–4 × greater than blue-green algal biomass, and the combined totals of these two groups have consistently provided more than 85% of the total phytoplankton biomass (Table 2).

The diatoms *Melosira granulata* (Ehr.) Ralfs and *M. ambigua* (Grun.) O. Müll have continued to dominate. The average 1985 *Melosira* biomass (9.5 mm^3·L^{-1}) was higher than values recorded for the May–October periods of all previous years (Fig. 3). Although much less dominant over the years, *Stephanodiscus* spp., mainly *S. astraea* (Ehr.) Grun. (see taxonomic footnote in Nicholls et al. 1986, p. 147), *S. hantzschii* Grun. and *S. invisitatus* Hohn and Helleman, have not increased. The average biomass of *Stephanodiscus* spp. during 1978–87 (0.37 mm^3·L^{-1}) was significantly less ($P < 0.05$) than the average (1.14 mm^3·L^{-1}) recorded for the pre-phosphorus control period of 1972–77.

The highest silicate levels were found in 1978 and 1979 immediately following phosphorus loading reductions; however, average silicate concentrations have declined again in recent years with the increased prevalence of *Melosira* (Fig. 3).

TABLE 2. Summary of May–October average phytoplankton as a percentage of total biovolume (dominant algal classes) at station B in the upper Bay of Quinte, 1972–87.

	Percentage of total					
Year	Cyanophyceae	Dinophyceae	Cryptophyceae	Chrysophyceae	Chlorophyceae	Bacillariophyceae
1972	17	3	3	<1	4	73
1973	20	6	4	1	3	66
1974	11	4	2	<1	2	82
1975	16	5	3	1	7	68
1976	22	1	3	1	4	70
1977	20	4	4	<1	6	65
1978	17	4	4	2	6	67
1979	27	4	3	<1	3	62
1980	21	2	6	2	4	65
1981	34	1	3	1	4	51
1982	13	1	2	<1	2	81
1983	21	<1	2	2	4	70
1984	39	1	3	1	2	54
1985	17	1	2	1	2	77
1986	27	<1	4	1	4	63
1987	40	3	4	<1	4	48

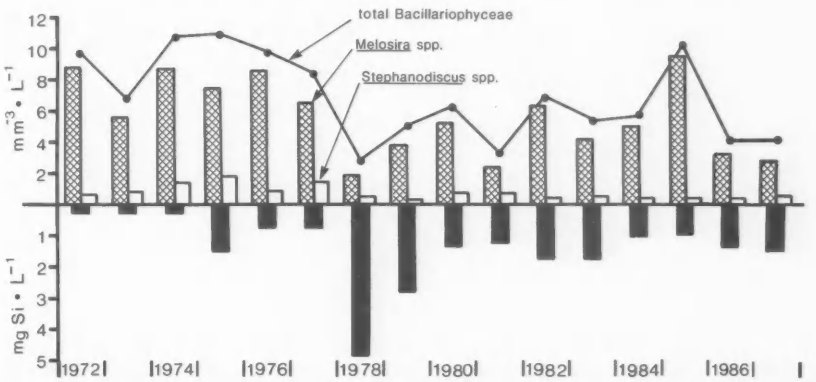

FIG. 3. Total Bacillariophyceae (diatom) biomass and the two major generic components, *Melosira* and *Stephanodiscus* over the May–October periods of 1972–87 at station B in the upper Bay of Quinte. Also shown are May–October average dissolved silicate levels (mg $Si \cdot L^{-1}$) over the same time period at station B.

Over the entire 16-yr period of observation, the nitrogen-fixing blue-green algae *Anabaena* and *Aphanizomenon* have been the most important elements of the cyanophycean flora, comprising between 54 (1975) and 95% (1981) of the total blue-green algal biomass. The lowest combined biomass of these two genera was found during 1978, the first year after significant point-source phosphorus loading reductions; the highest was found in 1987 (Fig. 4). Total nitrogen to total phosphorus ratios have increased significantly over the 1972–87 period (Fig. 4; $r = 0.884$); however, the contribution of nitrogen-fixing blue-green algae (*Anabaena* and *Aphanizomenon* spp.) to the total phytoplankton has not decreased as expected, but in fact has increased from 13.5% of the total during 1972–77 to 22% of the total during 1978–87.

While total phytoplankton and total phosphorus concentrations in the Bay of Quinte for the 1972–81 period were highly correlated when average data from all sampling stations were included ($n = 69$, $r = 0.90$; Nicholls et al. 1986, figure 15), similar highly significant correlations are not evident when more recent data are included and analyses are restricted to single stations. For example, at station B, $r = 0.604$ ($n = 16$). When these data are separated into pre- and postphosphorus removal time periods, correlation coefficients of -0.062 and 0.265 were determined for phytoplankton–total phosphorus relationships at station B for the 1972–77 and 1980–87 periods, respectively (Fig. 5a, 6a). In contrast, highly significant correlation coefficients ($P < 0.01$) were found for phytoplankton–fish relationships for the same two time periods ($r = 0.983$ and $r = 0.960$; Fig. 5b, 6b). Similar relationships were found for the phosphorus–phytoplankton–fish data from station HB in the middle bay for the 1972–78 period (Fig. 7).

Coincident with significant reductions in point-source phosphorus loadings in 1977 was a major collapse of both the white perch and alewife populations in the Bay of Quinte during the severe winters of 1976–77 and 1977–78 (Hurley 1986a, Ridgway et al. 1988). Although some recovery of these populations was noted, especially in 1979, 1981, and 1985, their numbers remained much below the pre 1977 levels. Large piscivores, in particular walleye (*Stizostedion vitreum*), became increasingly abundant in the upper bay after 1978 and continue to exert a significant pressure on alewife particularly, and on white perch to a lesser extent.

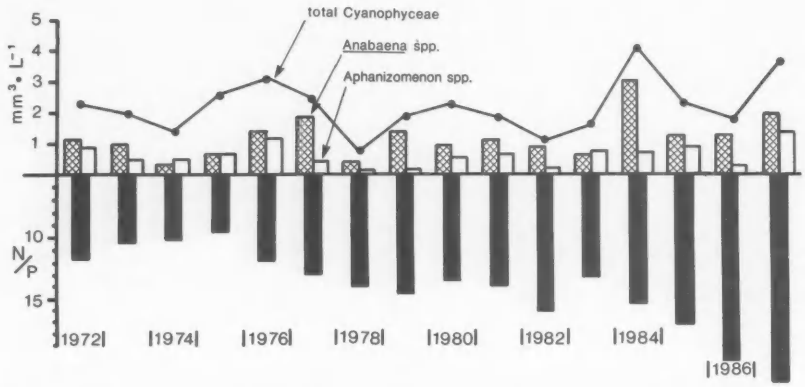

FIG. 4. Total Cyanophyceae (blue-green algae) biomass and the two major generic components, *Anabaena* and *Aphanizomenon* over the May–October periods of 1972–87 at station B in the upper Bay of Quinte. Also shown are total nitrogen to total phosphorus ratios (May–October averages) over the same time period at station B.

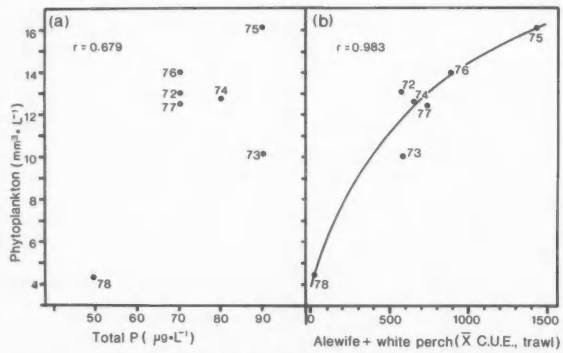

FIG. 5. Relationships between (a) May–October average phytoplankton biomass ($mm^3 \cdot L^{-1}$) and total phosphorus concentration ($\mu g\ P \cdot L^{-1}$) at station B in the upper Bay of Quinte 1972–78 and (b) average phytoplankton biomass at station B and mean catch per unit effort (C.U.E.) of alewife and white perch from standard bottom trawl drags in the upper Bay of Quinte. The line in (b) is from a least squares fit to a power curve, where $Y = 1.55\ x^{0.319}$. The correlation coefficient for the pre-phosphorus control period 1972–77 in (a) is $r = -0.062$.

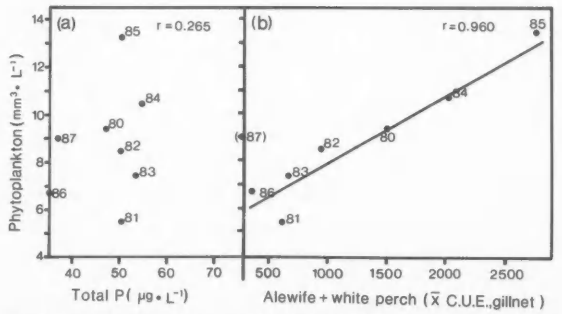

FIG. 6. Relationships between (a) May–October average phytoplankton biomass ($mm^3 \cdot L^{-1}$) and total phosphorus concentration ($\mu g\ P \cdot L^{-1}$) at station B in the upper Bay of Quinte 1980–87 and (b) average phytoplankton biomass at station B and mean catch per unit effort (C.U.E.) of alewife and white perch for standard experimental gill net lifts from the Bay of Quinte. Trawling was done only once in 1982 and gill nets were not set in the upper bay in 1985, so data from the middle Bay of Quinte gill net sets were used here. The position of the line and the correlation coefficient shown do not include the 1987 data in (b).

A suite of environmental variables in addition to total phosphorus and total nitrogen concentration, as well as white perch and alewife summer biomass was included in a stepwise regression with mean May–October phytoplankton biomass as the dependent variable. This analysis showed that July and August mean water temperature, total nitrogen concentration, white perch June–September mean biomass, and August water levels were significant parameters in the regression (Table 3). The model was highly significant with an adjusted R^2 of 0.825. These five variables generated a predictive equation with excellent agreement between fitted and measured phytoplankton for the upper bay (Fig. 8).

In spite of the excellent fit of predicted versus observed data in this series, there is strong evidence that total phosphorus (Nicholls et al. 1986) and alewife biomass (Hurley et al. 1986) are important parameters in explaining variations in phytoplankton biomass in the upper Bay of Quinte even though they were not significant according to the stepwise technique. Exam-

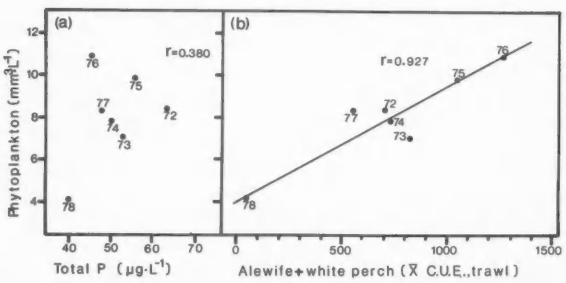

FIG. 7. Relationships between (a) May–October average phytoplankton biomass ($mm^3 \cdot L^{-1}$) and total phosphorus concentration ($\mu g\ P \cdot L^{-1}$) at station HB in the middle Bay of Quinte 1972–78 and (b) average phytoplankton biomass at station HB and mean catch per unit effort (C.U.E.) of alewife and white perch for standard bottom trawl drags in the upper and middle Bay of Quinte.

TABLE 3. Parameter estimates and analysis of variance for stepwise regression analysis of phytoplankton biomass on significant variables.

Variable	Parameter estimate	t	Probability parameter = 0
Intercept	605.131	3.152	0.010
August level	−7.524	−3.037	0.013
Total Nitrogen	0.016	3.425	0.007
White Perch biomass	0.095	5.295	0.0003
July temperature	−3.085	−4.475	0.001
August temperature	1.171	2.465	0.033

Analysis of variance

Source	*df*	Sum of squares	Mean square	*F*	Probability > *F*
Model	5	150.051	30.010	15.106	0.0002
Error	10	19.866	1.987		

Square root of mean square error = 1.409
Coefficient of variation (%) = 14.08

$R^2 = 0.883$; adjusted $R^2 = 0.825$

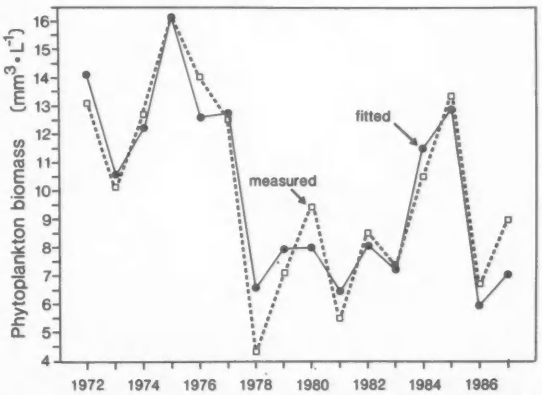

FIG. 8. Relationship between measured and fitted average May–October phytoplankton biomass in the upper Bay of Quinte 1972–87, based on a multiple regression model including five input variables of which white perch biomass explained more than 50% of the variance in the model (see Table 3).

ination of the correlation matrix for these variables however, showed that total phosphorus and total nitrogen were significantly correlated ($n = 16, r = 0.717, P = 0.002$), and that white perch biomass and alewife biomass were also significantly correlated ($n = 16, r = 0.555, P = 0.026$). This suggests that nutrient concentrations as well as fish biomass are important parameters and relatively slight changes in the values in the data set can determine which ones are entered in the final multiple regression.

Examination of the regressions resulting from all possible subsets of variables, where adjusted R^2 and Mallows' Cp statistic (Draper and Smith 1981) are calculated, showed that a set of variables including water temperature in some months, total phosphorus, total nitrogen, alewife and white perch biomass, and water levels in some months resulted in a regression with an adjusted $R^2 = 0.92$ and a Cp = 9.2. When the stepwise procedure was forced to include these variables some of the parameter estimates were not significant according to a '*t*' test.

As a further test of the significance of these parameters in a proposed model, a principal components analysis was done using all of the independent variables. The first four principal components were significant according to a scree test and explained 85% of the total variance. Table 4 shows that the first component includes significant positive correlations ($P < 0.01$) for water levels, alewife biomass, and total phosphorus, and a negative correlation with May temperature. The second component is positively correlated with white perch biomass, total phosphorus and total nitrogen, and spring (June) temperatures.

TABLE 4. Principal components analysis on the set of independent variables used in regression on phytoplankton biomass. Only those significant at $P < 0.01$ are shown ($df = 14, t = 0.623$).

Variable	First component	Second component	Third component	Fourth component
May temperature	−0.705			
June temperature		0.670		
August temperature			0.886	
September temperature				0.739
Total phosphorus	0.625	0.631		
Total nitrogen		0.659		
Alewife biomass	0.835			
White perch biomass		0.733		
May water level	0.749			
June water level	0.903			
July water level	0.958			
August water level	0.934			
September water level	0.852			

TABLE 5. Parameter estimates, significance measures, and analysis of variance of the stepwise regression analysis of phytoplankton biomass on principal components.

Variable	Parameter estimate	t	Probability $> t$
Intercept	10.013	15.913	0.0001
First component	1.332	2.049	0.0629
Second component	1.711	2.632	0.0219
Third component	−1.249	−1.923	0.0786

Analysis of variance

Source	*df*	Sum of squares	Mean square	F	Probability $> F$
Model	3	93.309	31.303	4.942	0.018
Error	12	76.008	6.334		

Square root of mean square error = 2.5268
Coefficient of variation (%) = 25.14

$R^2 = 0.553$; adjusted $R^2 = 0.441$

The third and fourth components include summer (August) and fall (September) temperatures only. Finally, the principal components were calculated for each year (1972–87) for which there were data and these values were used as independent variables with phytoplankton biomass as the dependent variable in a further regression analysis.

When phytoplankton biomass was regressed on these four principal components using a stepwise procedure, only the first three components were significant (Table 5). The second component entered the regression first and accounted for 26% of the variance. This component is a combination of white perch biomass, nutrient concentrations, and spring temperatures. The first component entered next as a combination of water levels, alewife biomass, total phosphorus, and early spring temperatures and accounted for 16% of the variance. The third component entered last and consisted of summer temperatures and accounted for 14% of the variance. In summary, this analysis points to the strong influence of water levels, nutrient concentrations, planktivore and benthivore biomass, and the lesser influence of water temperatures in accounting for variations in annual phytoplankton biomass.

Discussion

One of the most surprising findings of the long term phytoplankton data analyses from the upper Bay of Quinte relates to the lack of any significant changes in species composition despite a range in total biomass of about four-fold during the 16-yr period. Previous work by Tilman (1981), Smith (1983), and Sell et al. (1984) had suggested that shifts in dominance among blue-green algae and diatom species might have been expected given the observed changes in silicon to phosphorus and nitrogen to phosphorus ratios in the Bay of Quinte. However, the upper bay continues to be dominated by six or seven species of *Stephanodiscus*, *Melosira*, *Anabaena*, and *Aphanizomenon*, of which the mid-summer populations of *Melosira granulata* and *M. ambigua* are the most important. The proportion of the total phytoplankton contributed by the nitrogen-fixing *Anabaena* and *Aphanizomenon* species has actually increased, not decreased as expected, while nitrogen to phosphorus ratios increased from about 10 in the mid-1970's to 22 by 1987. The "critical threshold" concept (Smith 1983) may be important here and dramatic proportional declines in *Anabaena* and *Aphanizomenon* may not occur until nitrogen to phosphorus ratios approach 30.

Another surprising finding is the lack of any significant relationships between phytoplankton and phosphorus (whether phosphorus concentration or point-source phosphorus loading). While Nicholls et al. (1986) showed these relationships were significant when data from all sampling stations were pooled, the recent analyses restricted to single sampling stations and two separate time periods (pre- and post white perch and alewife die-offs), suggest that the recent changes in phytoplankton have been influenced by other factors as well as phosphorus. Similarly, Johnson (1986) has shown significant correlations between four algal related measures of response and point-source phosphorus load and percent point-source phosphorus load. However, most of the data points were grouped into two separate clusters for the pre- and postphosphorus removal periods (see Johnson 1986, figure 2). No significant correlations were found for the smaller data sets representing the separate pre- and postphosphorus removal periods. If phosphorus alone was the important variable, then significant relationships with phytoplankton should have existed for the two data subsets, prior to and after 1977. While phosphorus loading may determine the upper level of phytoplankton production and biomass accrual, planktivore and benthivore (especially white perch) biomasses, or factors correlated with these biomasses, clearly are important. Hypotheses are needed to explain the significance of the fish–phytoplankton relationship in the Bay of Quinte.

There is mounting evidence that fish predation in freshwater systems helps determine production and biomass at several levels of aquatic food chains (Shapiro 1980; Shapiro and Wright 1984; McQueen et al. 1986; Carpenter et al. 1985, 1987; Mills et al. 1987; Kitchell and Carpenter 1988; Northcote 1988). Because the control of phytoplankton biomass can be achieved by the combined effects of "bottom-up" (nutrient supply) and "top-down" (food chain) influences, it may not be instructive to apply simple linear regression models for these factors over the entire Bay of Quinte time series because the two major potential influences, phosphorus loading decreases, and white perch and alewife winter kill, both occurred in the late winters of 1977 and 1978.

In the shallow upper Bay of Quinte, planktivory and benthivory are two potentially important routes for biotic influences on phytoplankton. In their early life history, most of the abun-

dant fish species are zooplanktivores. However, prior to 1978, a major portion of total fish biomass in the upper bay was adult white perch. These fish are predominantly benthivores. Modest increases in their biomass were observed in some years after 1979, but they never reached the levels observed from 1972 to 1977.

If the major trophic influence of fish on phytoplankton in the Bay of Quinte is through planktivory, then there should be a negative correlation between phytoplankton and zooplankton. Zooplankton data are not available for all years of the Project Quinte investigation (Cooley et al. 1986); however, the recent data for the upper bay (J. Cooley, Department of Fisheries and Oceans, CCIW, Burlington, unpubl. data) show average biomass of total cladocera during 1982–86 was nearly two times higher than for the period 1975–76 and 1979–81. Hence, for 1979–81 versus 1982–86, these data do not fit the predation–grazing theory suggested by the fish phytoplankton relationships (however, they do fit for 1975–76 versus 1982–86).

Total cladoceran biomass in the upper bay has been dominated by small bodied forms, especially *Chydorus sphaericus* (Cooley et al. 1986), which have not been important food items for planktivores (Hurley 1986b). Also, *C. sphaericus* is unlikely to utilize large algae like *Melosira* spp. which dominate the Bay of Quinte. Large filter-feeding calanoids and cladocera are of much more potential significance as algal grazers and as food items for planktivorous fish than the smaller *Chydorus sphaericus*, *Bosmina*, and *Eubosmina* spp. (Carpenter et al. 1985). Moreover, even large bodied *Daphnia* species are not likely to utilize long *Melosira* filaments (Infante and Litt 1985).

The domination of the upper Bay of Quinte phytoplankton by large filamentous *Melosira* and blue-green algae may be impeding the development of significant *Daphnia* populations (along with the fish predation). Not only are these algae less desirable as food items, but at high density they can lead to reduced egg production and to generally reduced survival of juvenile *Daphnia* (Hartmann 1985; Vaga et al. 1985). If *Daphnia* become more abundant through changes in fish predation, some reductions in *Melosira* and blue-green algal biomass might result through the utilization of small elements of these algal groups (short filaments, hormogonia, auxospore germination products, etc.). However, because these algae comprise the bulk of the summer phytoplankton biomass, net changes in the total planktonic algal biomass would likely be small despite much greater utilization by *Daphnia* of the less well represented, but more "food-chain functional" cryptomonads, chrysomonads, and coccoid chlorophytes (Nicholls et al. 1986).

Hurley et al. (1986) noted a trend to greater biomass of larger zooplankton after 1977 and that these biomasses were negatively correlated with numbers of small fish taken in index trawls. These relationships apparently do not presently extend to the phytoplankton in the form of statistically significant negative correlations between phytoplankton and macrozooplankton, and may not in future, for reasons outlined above, unless other factors such as increasing nitrogen to phosphorus and silica to phosphorus ratios lead to changes in composition away from the dominance by *Melosira*, *Anabaena*, and *Aphanizomenon*.

A Benthic Link?

A lack of correlation between phytoplankton and macrozooplankton suggests that benthivory, and to a lesser extent planktivory, may be a more significant feature of the upper Bay of Quinte food web. White perch biomass was the most significant variable in the multiple regression analysis of factors controlling phytoplankton biomass (Table 3). These fish consume benthic oligochaetes and chironomids (Hurley 1986b) and Johannsson and Beaver (1983) have shown that *Melosira* was an important food item for benthic midge larvae in the Bay of Quinte. It is hypothesized that during summer calm periods, *Melosira* filaments settle to the sediments of the upper bay where they are consumed by midge larvae and other benthic organisms. Their resuspension into the plankton occurs through wind induced turbulence. The size of the *Melosira* population in the phytoplankton will therefore be controlled to some degree by the rate of loss through herbivory by benthic organisms during quiescent periods and this in turn may be controlled by the extent of benthic feeding by white perch.

In the recent past, the population of white perch in the Bay of Quinte declined dramatically from a peak in 1975 to a low in 1978 (Minns and Hurley 1986). Only 6 yr of chironomid biomass data are available (unfortunately not including either 1975 and 1978), and no significant correlations between chironomid biomass and white perch biomass are apparent. In the lower Bay of Quinte, the *Pontoporeia hoyi* population, which has been the most important food item for white perch in the lower bay, recovered after the collapse of the white perch (Johnson and McNeil 1986). In other systems where chironomids are the major food for fish, changes in fish feeding pressure are known to control chironomid production (Pechlaner and Zaderer 1985). So, although unproven at this point, the "benthic link" hypothesis seems realistic for the shallow upper Bay of Quinte.

It should be pointed out, however, that alewife biomass was a significant variable in the principal components analysis. This species, therefore, may play a significant biological role in the degree of phytoplankton biomass development through food web effects even though statistically its role did not appear overwhelming.

The importance of the point-sources of phosphorus loading relative to the diffuse inputs has been demonstrated for the Bay of Quinte. Significant correlations were found between independent trophic state variables and point-source loading, but not with total phosphorus load (Johnson 1986). The return to much higher phytoplankton biomass in recent years has occurred despite continued success with the phosphorus control programme at municipal wastewater treatment plants discharging to the Bay of Quinte. During 1985, point-source loadings of total phosphorus were the lowest on record, yet *Melosira* biomass was the highest recorded since 1972. Phosphorus concentrations averaging less than 50 $\mu g\ P \cdot L^{-1}$ (in contrast to 70–90 $\mu g\ P \cdot L^{-1}$ during 1972–77) during the May–October periods of 1978–85 were consistent with these reduced loadings. Point-source loading was higher in 1986 than in 1985 (G. Owen, Ontario Ministry of the Environment, Kingston, Ont., unpubl. data) but because of unusually high flows from the Trent River (B. Kitchen, Environment Canada, Peterborough, Ont., pers. comm.) the resultant high dilution contributed to the lowest average total phosphorus concentration yet observed in the upper bay (33 $\mu g\ P \cdot L^{-1}$).

Planktonic algae respond to phosphorus concentrations created by the combined effects of phosphorus and water loading. Phosphorus concentration sets the upper limits on phytoplankton biomass, while other factors such as herbivore grazing and displacement or dilution effects on algal cells determine the

extent to which these upper limits are realized. Measurements of phosphorus concentration in the Bay of Quinte, therefore, integrate the measures of phosphorus load and water load; however the direct effects of flow and water level changes on phytoplankton are not readily quantified.

For the relatively shallow upper bay, August mean water level (correlated with summer Trent River flow) was an important variable in the multiple regression phytoplankton model and conceptually supports the "benthic link" hypothesis. Water levels were also a significant component in the principal components analysis. Weather induced alteration of quiescent and turbulent conditions in the upper bay would be less effective in the transfer of *Melosira* between benthic and planktonic zones during high water level years than during low water level years when resuspension of *Melosira* per unit of turbulent energy input would be more efficient. The difference between high and low water levels is also likely great enough (20% of mean) to be a significant influence on phytoplankton density and residence time through dilution and flushing effects (a negative correlate in the model).

There may be some danger in assessing the long-term May–October average effects of hydrology, herbivory, and phosphorus load on phytoplankton biomass because each of these controlling factors may be dominant influences for only short time periods during the growing season. However, the evidence suggests that average abundance of certain fish stocks in the Bay of Quinte may be a very important factor for the indirect control of average May–October phytoplankton biomass. This is supported by recent studies elsewhere in the Great Lakes. In Lake Michigan, changes in alewife populations and densities of zooplankton and phytoplankton (Edgington 1985; Scavia et al. 1986; Evans 1986) suggest that trophic interactions may be a very significant feature of large lakes.

It is apparent that the implications of the recent Project Quinte findings are potentially very important. It is possible that in many situations, control of eutrophication problems (e.g. blooms of potentially toxic blue-green algae, bad taste and odour in drinking water supplies, depreciation of high quality recreational swimming opportunities, etc.) cannot be achieved by reduced nutrient loading alone but, rather, must depend on the combined effects of nutrient loading control and management of fish habitat and fish community structure.

In the Bay of Quinte, reestablishment of a stable fish community dominated by desirable predator species (the larger piscivorous percids, centrarchids, and esocids) may also depend on the reestablishment of extensive macrophyte beds in the Bay of Quinte. These plant communities were lost from large areas of the upper bay 20–30 yr ago, presumably as a consequence of proliferation of phytoplankton and a resultant "shade-out" effect. Experimental and management procedures designed to accelerate the recolonization by macrophytes and enhance shoreline pike (*Esox lucius*) habitat should be a major thrust of the Bay of Quinte management plan of the future. It is also apparent that the role of food chain interactions in controlling some symptoms of Bay of Quinte eutrophication needs to be better understood so that the greatest potential benefits of reduced phosphorus loading can be achieved by simultaneous management of other components of the Bay of Quinte ecosystem.

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Fixation Artifacts in Rainbow Trout (*Salmo gairdneri*) Gills: A Morphometric Evaluation

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Speare, D. J., and H. W. Ferguson. 1989. Fixation artifacts in rainbow trout (*Salmo gairdneri*) gills: a morphometric evaluation. Can. J. Fish. Aquat. Sci. 46: 780–785.

Epithelial capillary separation (E.C.S.) and epithelial cell hypertrophy (E.H.) of the gill lamellae of fish are two histopathological changes frequently described in association with toxic insults. Both of these gill changes increased in a significant linear manner over delay periods of 20–900 s from death to first entering either Bouin's or 10% formalin fixative. E.C.S. also occurred rapidly when gills were examined as whole mount preparations. The presence of occasional necrotic epithelial and chloride cells resembled apoptosis and is not in itself abnormal, nor did the type of fixative used or fixation delay have an effect on their extent. Gills from fish killed by either MS-222 or cervical spinal severance were similar, except that the latter also had multifocal lamellar telangiectasis. We conclude that E.C.S. and E.H. are readily mimicked by preparation and postmortem artifacts that occur rapidly after death when this is caused by either MS-222 or spinal severance. Bouin's fixative should be used to minimize these changes.

La séparation des capillaires épithéliaux (S.C.E.) et l'hypertrophie des cellules épithéliales (H.C.E.) des lamelles des branchies des poissons sont deux modifications histopathologiques décrites fréquemment en association avec les agressions toxiques. Ces deux modifications des branchies ont augmenté de façon linéaire au cours de périodes de 20–900 s qui s'écoulaient entre la mort et l'immersion dans le fixateur de Bouin ou la formaline à 10%. La S.C.E. se produisait également rapidement dans les préparations microscopiques de branchies entières. La présence occasionnelle de cellules épithéliales nécrotiques et acidogènes ressemble à une apoptose et n'est pas anormal en soi; elle n'est pas non plus influencée par le type de fixateur utilisé ou par le temps de fixation. Les branchies des poissons tués par le MS-222 ou par un coup porté à la colonne cervicale étaient similaires, sauf que les dernières présentaient également des télangiectasies lamellaires multifocales. Nous concluons que la S.C.E. et l'H.C.E. sont des modifications qui peuvent être imitées par la préparation et les artéfacts postmortem, lesquels se produisent rapidement lorsque la mort est causée par le MS-222 ou un coup porté à la colonne cervicale. Il faudrait utiliser le fixateur de Bouin pour minimiser ces changements.

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Fish gills are frequently used for assessing the pathological effects of water-borne pollutants (Mallatt 1985). In Mallatt's review of these studies, commonly reported gill lesions were lamellar epithelial lifting (epithelial capillary separation, E.C.S.), lamellar epithelial necrosis (E.N.), and lamellar epithelial hypertrophy (E.H.). Less commonly reported was chloride cell necrosis (C.C.N.). The literature frequently indicated widely differing extent and intensity of E.C.S., E.H., and E.N. within a single fish, between different fish in a given exposure condition, and in controls.

With light microscopy (L.M.) E.C.S. appears as an edematous lifting of the lamellar epithelium from the pillar cells (Eller 1975; Roberts 1978; Mallatt 1985). With electron microscopy (E.M.) it is more accurately defined as edema of tissue spaces between the double layered lamellar epithelium (Rhodin 1964; Perry et al. 1984; Albassam et al. 1987). Necrosis has been described at the L.M. level by tinctorial changes, along with nuclear pyknosis, karyorrhexis, and karyolysis (Benville et al. 1968). E.H. at the L.M. level describes cytoplasmic and nuclear swelling of epithelial cells. (Roberts 1978; Mallatt 1985).

Postmortem tissue changes (autolysis), are often difficult to differentiate from pathological changes. Rapid fixation is especially necessary for fish tissues which undergo accelerated decomposition (Roberts 1978). Several authors (Walsh and Ribelin 1975; Grizzle 1981; Wobeser 1975; Hughes et al. 1979) described the occurrence of E.C.S. and/or E.H. as a terminal or autolytic event. This is similar to our experience with diseased and control fish submitted to the Fish Pathology Laboratory, at the Ontario Veterinary College.

The purpose of this study was to determine the effect of delays between death and initial exposure of gill tissue to fixatives commonly used in fish research (Bouin's and 10% formalin), on the presence and extent of E.C.S., E.N., E.H., and C.C.N. A comparison of fixative effects was also done.

Materials and Methods

Fish

Juvenile 6–7 g rainbow trout, *Salmo gairdneri*, were supplied from a local specific pathogen-free fish farm. During a 3-mo monitoring period at the farm site no diseases or gill changes were found, and water quality parameters were normal with minimal fluctuation.

After transport to the Ontario Veterinary College, the fish were maintained in 400-L fiberglass circular units holding 1000 fish each, fed a commercial diet, and monitored histologically for disease or gill changes. Flow rate to the individual units was 2.8 $L \cdot min^{-1}$, temperature was 12°C, pH range of 7.9–8.1, total ammonia of 0.1 $mg \cdot L^{-1}$, turbidity of zero, and dissolved oxygen range of 6.8–7.2 $mg \cdot L^{-1}$.

Fixatives

Two fixatives were used: Bouin's fixative (picric acid 9.5 g, trichloroacetic acid 2.2 g, and formaldehyde solution 210 mL, Harleco Diagnostics, B.D.H. Chemicals, Toronto, Ontario), and phosphate buffered 10% formalin, with final tested pH of 7.0. Both fixatives were used at 20°C. The minimum ratio of fixative to tissue was 10:1 (vol/vol).

Tissues fixed in Bouin's were transferred to 70% ethyl alcohol after 48 h where they remained for 24 h. Those in 10% formalin were fixed for 72 h. The first gill arch from the exposed (right) side of the fish was removed without touching the lamellae, placed in a cassette, washed, dehydrated, embedded in paraffin, sectioned at 4–6 μm and stained with hematoxylin and eosin (Thompson and Hunt 1966).

Design

Fish were randomly assigned to one of six treatments consisting of a posteuthanasia fixation delay of 20, 300, or 900 s followed by immersion in either Bouin's or 10% formalin fixative. Six fish were assigned to each of the six types of treatments. For each fish, the entire process of killing, opercular removal, time delay, and placing into individual jars of fixative, was completed before the next fish was removed from the holding unit and assigned to its treatment.

Trout were killed individually in a 250-$mg \cdot L^{-1}$ solution of tricaine methanesulfonate (MS-222). Respiratory and other movements ceased in 20–40 s, whereupon the fish was removed, and the operculum on the right side excised. This process took from 15–20 s, and represented the total delay time for those fish assigned to the 20-s fixation delay. Fish assigned to the 300 and 900 s fixation delay groups were placed on their left sides on a wet stainless steel surface at room temperature (17°C), until the fixation delay period had elapsed, and then immersed in fixative.

Fish killed by cervical spinal severance were also examined. Whole mount gill preparations suspended in water were observed by light microscopy for the development of E.C.S. and E.H.

Morphometric Evaluation

Lamellae from three well-oriented filaments of the first gill arch from each fish were assessed. Suitable filaments were chosen from the ventral, middle, and dorsal areas of the arch. Well-oriented describes those filaments with lamellae of equal length bilaterally present to near the tip of the filament, and with well defined interlamellar zones.

For each filament evaluated, the following parameters were assessed by L.M.: (1) E.C.S. as the percent of lamellae affected, (2) E.N. as the percent of lamellae with one or more affected epithelial cells, (3) E.H. as the percent of lamellae with at least two hypertrophied or swollen epithelial cells. (4) C.C.N. as the percent of interlamellar spaces with one or more affected chloride cells.

TABLE 1. Mean $\bar{x}$ and standard deviation (SD) of MS-222 killed, Bouin's and 10% formalin fixed treatment groups for epithelial capillary separation (E.C.S.), epithelial necrosis (E.N.), epithelial cell hypertrophy (E.H.), and chloride cell necrosis (C.C.N.). For each value $n = 6$.

Fixative	Fixative delay (s)	E.C.S.(%)	E.N.(%)	E.H.(%)	C.C.N.(%)
Bouin's	20	5.03 (4.34)	2.60 (1.20)	3.73 (1.74)	4.22 (1.84)
	300	29.15 (5.69)	16.41 (2.78)	34.60 (2.76)	13.40 (2.76)
	900	45.60 (6.30)	18.80 (2.61)	50.60 (2.78)	13.60 (2.88)
Formalin	20	22.95 (9.44)	10.10 (0.84)	20.10 (6.90)	7.76 (2.67)
	300	36.50 (3.33)	16.13 (3.84)	46.10 (5.36)	14.70 (6.90)
	900	90.42 (10.42)	12.25 (3.80)	91.76 (8.50)	8.59 (1.73)

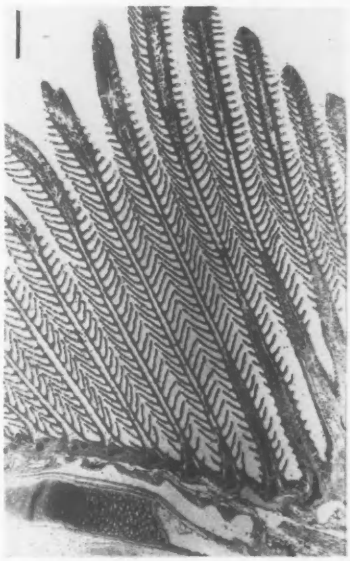

FIG. 1. Portion of a gill from a rainbow trout, fixed in Bouin's after a 20-s fixation delay. Lamellae are normal, epithelial capillary separation (E.C.S.) and epithelial cell hypertrophy (E.H.) are absent. Bar = 260 μm.

Statistical Evaluation

Parameter values for a given fish were expressed as pooled means from the three filaments used. From this, a group mean was determined for the six fish in each treatment group. Fisher's protected least significant difference (L.S.D., Snedecor and Cochrane 1980) was used to assess whether significant differences ($p < 0.05$) were present in the overall model, and for class effects (fixative, and time). Specific predetermined contrasts of treatment groups were then made using ANOVA.

The effect of delayed fixation was determined using simple linear regression. A t-test was used to determine the significance of the slope. Goodness of fit was determined using Pear-

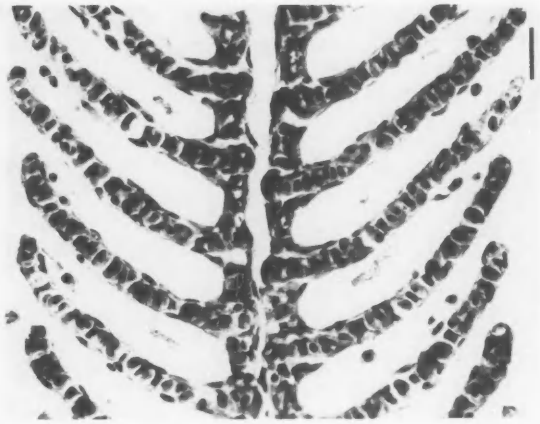

FIG. 2. Higher power of filament from Fig. 1 showing several normal lamellae covered by a closely apposed layer of flat lamellar epithelial cells. Bar = 25 μm.

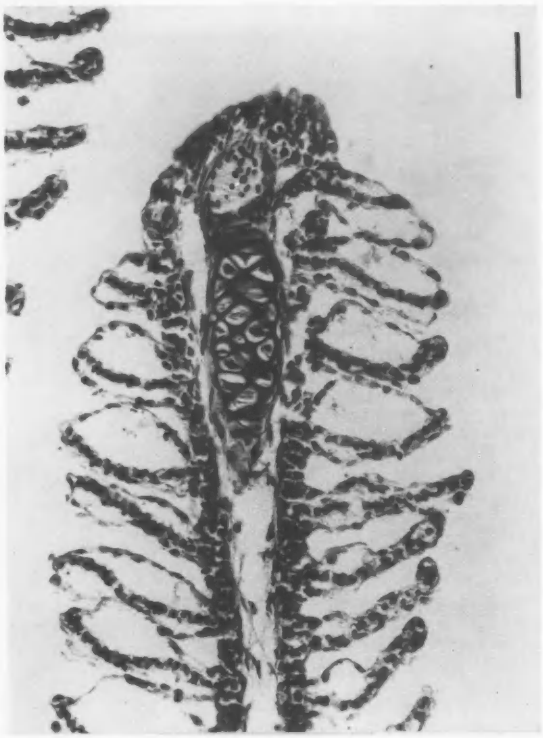

FIG. 3. Widespread epithelial capillary separation (E.C.S.) distally on a filament. From a fish immersed in 10% formalin fixative after a 900-s fixation delay. Note also the dilated extracellular spaces in the filament. Bar = 50 μm.

son's correlation index (R), and the co-efficient of variation (C.V.).

All statistical procedures were done using SAS programs (SAS Institute Inc., Cary, NC, USA).

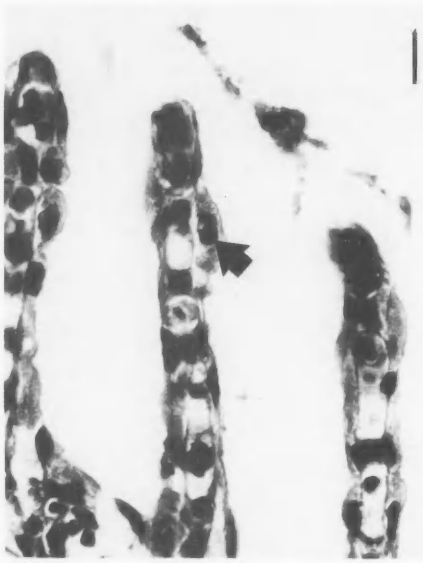

FIG. 4. Enlarged nucleus of a swollen lamellar epithelial cells (arrow). From a fish immersed in 10% formalin fixative after a 300-s fixation delay. Bar = 12.5 μm.

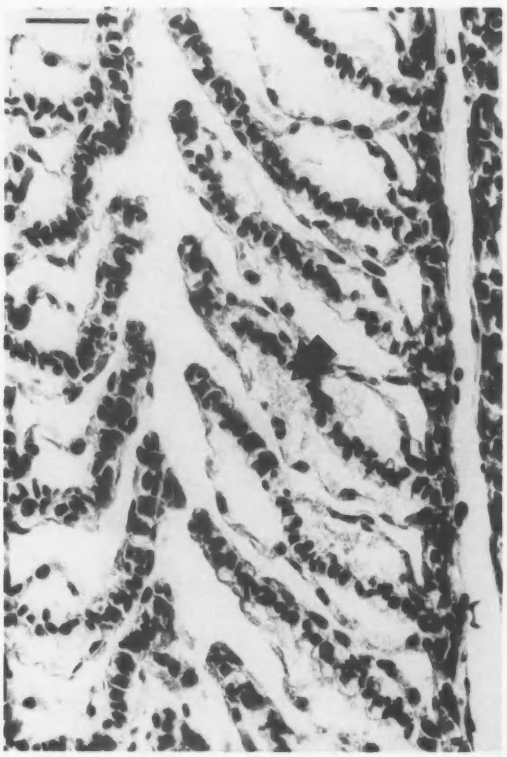

FIG. 5. Widespread epithelial cell separation (E.C.S.) mid-way along a gill filament. Material resembling protein (arrow) is in the extracellular spaces. From a fish immersed in Bouin's fixative after a 900-s fixation delay. Bar = 15 μm.

FIG. 6. An enlarged necrotic chloride cell (arrow) in an interlamellar position with marked granularity of the cytoplasm and karyorrhexis. From a fish immersed in Bouin's fixative after a 300-s fixation delay. Bar = 9 μm.

FIG. 7. Gill whole mount with areas of epithelial cell separation (E.C.S.) developing in less than 1 min after death. Bar = 25 μm.

Results

General Histological Feature

With both fixatives and with both methods of killing, gills subjected to a 20-s fixation delay rarely had E.C.S. or E.H. (Fig. 1 and 2; Table 1). These features were frequently present on gills with a 300 or 900-s fixation delay (Fig. 3 and 4; Table 1). A pale eosinophilic matrix was variably present in the enlarged tissue spaces created by E.C.S. (Fig. 5). Expansion of intercellular spaces of the filamental epithelium adjacent to areas of E.C.S. was extensive in gills subjected to a 900-s fixation delay (Fig. 3).

E.C. and C.N.N. were occasionally seen in gills from all treatment groups (Fig. 6; Table 1). Gills from all treatment groups were otherwise normal except for occasional lamellar aneurysms in those killed by cervical spinal section.

Gill tissues mounted whole in water also developed E.C.S. (Fig. 7). Multifocal areas of separation developed in less than 1 min after death. This began at the base of lamellae, and progressed toward the lamellar tip. Lamellar epithelial cells rapidly became markedly swollen.

General Observations on Treatments

Significant differences ($p < 0.01$) were present between treatments attributed to the effects of fixatives and different fixation time delays for E.C.S. and E.H. For E.N. and C.C.N. however, differences were present between treatments attributable to fixation time delays only.

Fixation Effects

A contrast of Bouin's and formalin fixed tissues (Table 1), using the double sided *t*-test of the least square means of data grouped over the three fixation delays indicated the following. Compared with Bouin's, formalin fixed gill tissues had a significant increase in the percentage of lamellae with E.C.S. (49.7 versus 26.6%, $p < 0.01$). This was also true for E.H. (52.7 versus 29.7%, $p < 0.01$). There were no significant differences between fixatives for the extent of E.N. or C.C.N.

Fixation Delay Effects

For Bouin's and formalin fixed gill tissues (Table 1), significant stepwise increases in E.C.S. and E.H. occurred with increases in fixation delay ($p < 0.01$), except for the contrast of E.C.S. for formalin fixed gills at 20 and 300 s, which was significant at $p < 0.1$ only. For both fixatives the relationship of the percentage of lamellae with E.C.S. and E.H. to fixation delay (seconds) was linear, with significant positive slope and strong correlation. Results of regressions are as follows. Considering E.C.S. first, Bouin's fixed tissues had a slope of 0.043 ($p < 0.01$), with a correlation index of 0.91 and C.V. of 28.8. Formalin fixed gill had a slope of 0.079 ($p < 0.01$), a correlation index of 0.96, and C.V. of 17.84. For E.H., Bouin's fixed tissues had a slope of 0.049 ($p < 0.01$), correlation index of 0.88 and C.V. of 33.75. Formalin fixed tissues had a slope of 0.081 ($p < 0.01$), a correlation index of 0.976, and C.V. of 13.27.

For E.N. and C.N.N., no regression effect was demonstrated for either fixative. Significant ($p < 0.01$) differences did however exist between some parameter means (Table 1) with different time delays of fixatives. For Bouin's and formalin fixed gills, E.N. was significantly less at 20 s than at either 300 or

900 s fixation delay. No difference was present between 300 and 900 s delay. For Bouin's fixative, C.C.N. was significantly less at 20 than at 300 and 900 s although no difference existed between 300 and 900 s. For formalin fixed tissues, the only significant difference was less C.C.N. at 20 than at 300 s.

Discussion

We have shown that marked differences in the morphological features of gill tissues, especially E.C.S. and E.H., occur with the use of different fixatives (Bouin's versus 10% formalin) and with different fixative delay periods. Bouin's fixative, rather than 10% formalin minimized E.C.S. and E.H. artifact. This study also shows that since healthy rainbow trout can have E.C.S. and E.H. as a peri-mortem event, even when tissue fixation commences as soon as 20 s after death, the mere presence of these changes therefore is not necessarily pathological. This is further supported by the observed development of these changes during whole mount examination.

Our results support work by Walsh and Ribelin (1975) and Grizzle (1981) who described the artifactual occurrence of E.C.S. and E.H. which mimicked pathological change. Grizzle (1981) defined E.C.S. as significant (pathologically) only when it affected greater than 20% of the gill. Walsh and Ribelin (1975) further defined true (pathological) E.C.S. as having eosinophilic material resembling protein in the created tissue space. Similar eosinophilic material however was also seen sporadically in our study and may not always therefore be pathological.

At the L.M. level, it is difficult to differentiate hypertrophy from hydropic degeneration of epithelial cells (each word implying a distinct pathogenesis). The dramatic increase in the number of swollen cells with increasing fixation delay suggests that the process is hydropic degeneration. Pathological as well as peri-mortem lamellar edema may cause swelling of lamellar epithelial cells in a manner similar to hydropic degeneration of alveolar epithelial cells in mammals with alveolar edema (Robin et al. 1973). This could explain the parallel between E.C.S. and E.H.

Perry et al. (1984) described the build-up of lamellar extracellular fluid as a normal event. This is supported by recent work which showed that protein permeability through systemic capillaries is very high in fish (Nichols 1987). Hargens et al. (1974) described pillar cell permeability as being similar to systemic capillaries. Perry et al. (1984) commented that the lack of normal breathing kinetics and muscular tone may create the high incidence of E.C.S. encountered as an artifact in gill perfusate studies. When fish are killed, respiratory movements cease before cardiac contractions cease, perhaps contributing to peri-mortem lamellar edema in a similar manner to the lamellar edema seen with perfusate studies.

Our study also shows that edema of filamental epithelium occurred in areas adjacent to severe E.C.S. Laurent (1984) showed that filamental and lamellar extracellular spaces are continuous and connect with the central venous sinus. The presence of the artifactual E.C.S. and filamental edema occurring together may therefore simply represent anatomically continuous regions of edema.

In a homologous system, the lung, capillary permeability and alveolar edema can be promoted by decreased interstitial pressure brought about by sudden abnormal changes in surface tension and baric pressure, such as with rapid removal of pleural effusions (Robin et al. 1973; West 1981). Lamellar edema may similarly be promoted by decreased interstitial pressure. This could readily occur when fish are removed from water for post-mortem dissection and the gills exposed to air. Air exposure subjects the gills to dramatic density, baric, and surface tension changes (Dejour 1981; Randall et al. 1981). This could reduce interstitial pressure enough to promote lamellar edema.

As also reported by Herman (1985), spinal severance of our fish caused lamellar telangiectasis. Its cause is unknown, but it may prove to be related to extreme sympathetic vasomotor events.

Some significant differences existed between treatments for the presence of E.N. and C.N.N., but conclusive trends were not established. The study does nevertheless indicate that occasional necrotic cells can be present in normal gill tissues. This is only to be expected when the high turn-over rate of these cells is considered (Zenker et al. 1987; Chretien and Pisam 1986) and resembles the process of apoptosis for lamellar epithelial cells described by Daoust et al. (1984).

Artifacts can easily develop in fish gills. These changes can mimick pathology. In comparing the gills of fish from different treatment groups (especially for the presence of E.C.S. and E.H., and also for E.N. and C.C.N.) strict standardization of killing and processing is necessary. Bias due to fixation delay could occur in experimental protocols which compare groups of fish which die during an exposure period with euthanized controls, or where extensive dissection or measurement of fish delays fixation. When fish are killed in groups rather than one at a time, variable fixation delay within the group is unavoidable. A postmortem technique oriented toward achieving a known standard and short fixation delay for all groups in the study is necessary when gills are intended to be a major organ of examination.

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Temperature Requirements in Atlantic Salmon (*Salmo salar*), Brown Trout (*Salmo trutta*), and Arctic Char (*Salvelinus alpinus*) from Hatching to Initial Feeding Compared with Geographic Distribution

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Jensen, A. J., B. O. Johnsen, and L. Saksgård. 1989. Temperature requirements in Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and Arctic char (*Salvelinus alpinus*) from hatching to initial feeding compared with geographic distribution. Can. J. Fish. Aquat. Sci. 46: 786–789.

Development time at different temperatures from hatching to 50% feeding was studied in Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) alevins. Live animals were used as food. In both species the development time decreased with increasing temperature, and these relationships were described by power curves. The results were compared with similar data for Arctic char (*Salvelinus alpinus*). At temperatures above about 8°C, the development time to 50% feeding was the same for all three species. However, at lower temperatures Atlantic salmon alevins needed more time to reach the stage of initial feeding than did Arctic char. Brown trout were intermediate. These results are in accordance with the known optimum temperature ranges for the three species and their geographic distribution.

On a étudié, chez le saumon Atlantique (*Salmo salar*) et chez la truite brune (*Salmo trutta*), la durée du développement à différentes températures, de l'éclosion au stade où 50 % des individus s'alimentent. Les animaux vivants ont servi de nourriture. On a constaté chez ces deux espèces une diminution de la durée du développement à la suite d'une augmentation de la température et on a représenté ces relations par des courbes de puissance. Les résultats ont été comparés à des données semblables obtenus avec l'omble chevalier (*Salvelinus alpinus*). À des températures supérieures à 8°C, la durée du développement jusqu'au stade où 50 % des individus s'alimentent a été la même pour les trois espèces. Cependant, à des températures inférieures, il fallait plus de temps aux alevins de saumon Atlantique pour atteindre le stade du début de l'alimentation, comparativement aux alevins d'omble chevalier. La truite brune a donné des résultats intermédiaires. Les résultats concordent avec les plages de température optimales connues pour les trois espèces et avec leur répartition géographique.

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Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) eggs are normally deposited at depths from 5 to 30 cm in gravel in the streambed. After hatching, alevins remain covered by gravel for several weeks, during which time they survive on nutrients from their large yolk sacs. Some time before the yolk is exhausted, alevins start exogenous feeding.

The point at which active feeding normally begins in salmonids is important. Environmental factors such as water flow, water temperature, and food supply must be favourable for the alevins to survive this sensitive stage. Assessment of the influence of changes in these factors on the starting point of active feeding is particularly significant in regulated rivers where water temperature or water flow regime may be altered. It is known that timing of emergence may influence subsequent survival (Bams 1969; Mason 1976; Godin 1980).

In this study we investigated the time taken from hatching to 50% feeding in Atlantic salmon and brown trout alevins reared at different constant temperatures, using live insect larvae as food. Corresponding data (Wallace and Aasjord 1984) for Arctic char (*Salvelinus alpinus*) are also included. These species are the only three naturally occurring, anadromous salmonids found in Norwegian salmon rivers. We found considerable differences in temperature requirements between these three species in the study period. Therefore, we compared the results with the geographic distribution of the species, as well as with their optimum temperature ranges.

Methods

In seven experiments on Atlantic salmon and four on brown trout we used specimens from the populations in the River Vefsna. In addition, Atlantic Salmon eggs from Lundamo hatchery in central Norway were used in two experiments.

For each of the 13 experiments 100 alevins were collected from a bulk supply of hatching eggs. All the alevins hatched on the same night and were transferred within 24 h to 0.5-L perforated bottles maintained at the test temperatures. Unfiltered water from the city of Trondheim water supply was used, and the water flow was 0.6 $L \cdot min^{-1}$ or more. The alevins were kept in the dark except during feeding.

Ten alevins were chosen at random from a bottle for each feeding test and transferred to the experimental aquarium along with 100–200 black, living mosquito (Culicidae) larvae. An air pump aerated and circulated the water in the plexiglass aquar-

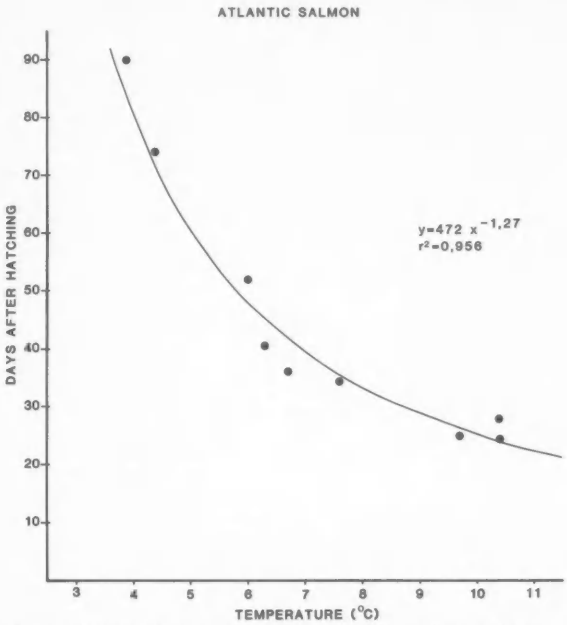

FIG. 1. Number of days from hatching to 50% feeding in Atlantic salmon alevins at different temperatures.

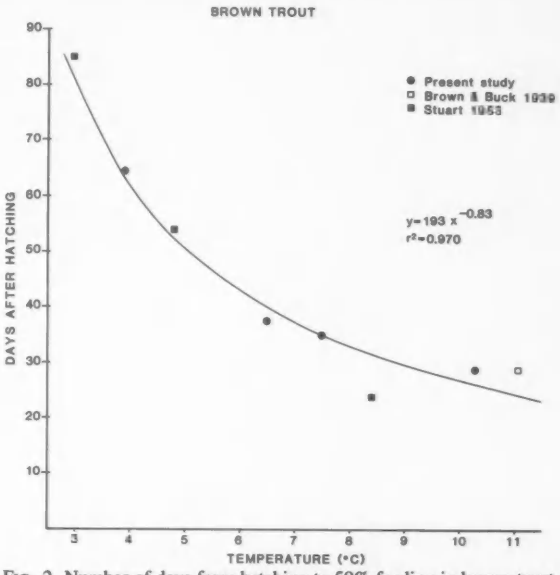

FIG. 2. Number of days from hatching to 50% feeding in brown trout alevins at different temperatures. Our data are compared with those published by Brown and Buck (1939) and Stuart (1953). The equation calculated is based on data from the present results only.

ium, which measured 35 × 2.5 × 20 cm (length, width, height). The bottom was covered by a 4-cm thick layer of gravel, mainly composed of particles sized 1–2.5 cm, and this part of the aquarium was also covered by black tape to reduce the light intensity in the gravel. The air pump circulated the mosquito larvae in the water as well as in the gravel.

Each feeding test lasted for 2 h, following which the alimentary tract of each alevin was examined for food particles. Ingested food was easily detected because of the black colour of the mosquito larvae. After examination the alevins were returned to the bottle. The 50% point was established by linear interpolation.

In the seven experiments with Atlantic salmon from the Vefsna population, the mean ±SD daily water temperatures from hatching to 50% feeding were as follows: 3.9±0.63, 4.4±0.63, 6.0±0.24, 6.7±0.24, 9.7±0.59, 10.4±0.70, and 10.4±0.70 °C. The two experiments with eggs from the Lundamo hatchery were conducted at 6.3±0.21 and 7.6±0.10 °C. In the four experiments with brown trout, mean daily water temperatures were 3.9±0.62, 6.5±0.38, 7.5±0.39, and 10.3±0.70 °C.

Allen (1940, 1941) observed that juvenile Atlantic salmon in two British streams moved from riffles to pools at temperatures below 7°C, and reduced or stopped feeding. The lower limit for growth of Atlantic salmon in Norwegian rivers also seems to be about 7°C (Jensen and Johnsen 1986). Experiences from Norwegian salmon farming have demonstrated that for successful initial feeding of salmon, temperatures should be above about 8°C (Refstie 1979). For this reason we carried out the feeding tests at a water temperature above this critical level. To ensure success, we started each feeding test at water storage temperatures, and did not control temperature during any of the 2-h tests. The room temperature (16–18°C) was always higher than that in the test aquarium, and hence, the latter temperature

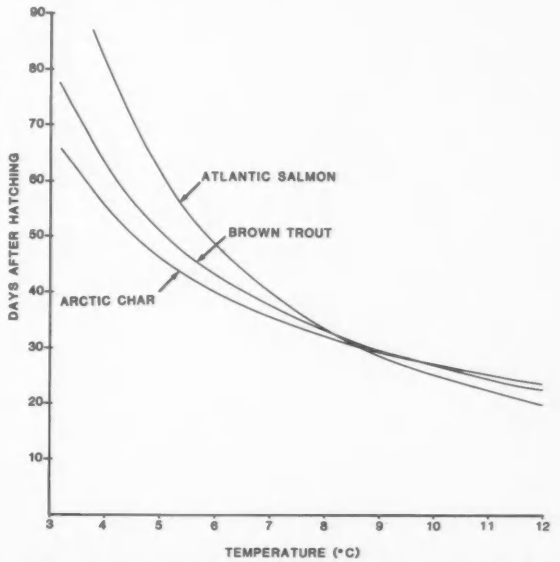

FIG. 3. Number of days from hatching to 50% feeding for alevins of Atlantic salmon, brown trout, and Arctic char at different temperatures. The last one is constructed from data published by Wallace and Aasjord (1984) by the method of least squares.

increased during the test. Test measurements showed that after 0.5 h 25% of the initial temperature difference was smoothed. The corresponding fraction was 42, 56, and 66% after 1, 1.5, and 2 h, respectively. For this reason the effective feeding period was about 0.5 h shorter for fish stored at the lowest compared with the highest temperature.

Results and Discussion

In both Atlantic salmon and brown trout the length of the period from hatching to 50% feeding decreased with increasing temperature (Fig. 1, 2). By the method of least squares the power curve proved the best fit to the present data for both Atlantic salmon and brown trout. The calculated equations are given in the figures.

The relationship between temperature and hatching time for the eggs of salmonids is also best described by power curves (Crisp 1981). Humpesch and Elliott (1980) pointed out that the power law appears to adequately describe egg development in a wide range of aquatic animals. For some salmonids the time taken from hatching to 50% emergence is also well described by this law (Crisp 1988). Hence, the results obtained support the use of 50% feeding as a valid stage of development.

Data from two similar experiments on brown trout are shown in Fig. 2 (Brown and Buck 1939; Stuart 1953). While we used live food, the other two investigations used finely ground beef liver and fish liver, respectively. Figure 2 demonstrates that brown trout alevins start feeding at the same time regardless of whether they are offered living or nonliving food. These results agree with Stuart (1953), who in some experiments offered nonliving and living food to brown trout alevins at the emergence stage. For both food types only moving food particles were seized. MacCrimmon and Twongo (1980) studied initial feeding behavior of rainbow trout (*Salmo gairdneri*) by feeding live brine shrimp nauplii and dry food rations. One or two days after swim-up they began to react to almost any drifting particle within about two body lengths. However, it was apparent that recognition and acceptance of mobile live food was greater than that of dry rations.

Reports in the literature differ widely concerning the onset of exogenous feeding in salmonids. Some authors believe feeding may actually begin before emergence is completed (Disler 1953; Stuart 1953; Dill 1967; Thomas and Shelton 1968; Gustafson-Marjanen and Dowse 1983; Field-Dodgson 1988). Other studies relate initial feeding to a wide variety of events. These include emergence from the gravel redd (Brown and Buck 1939; Mason 1976; Twongo and MacCrimmon 1976), or shortly after that stage (Bams 1969; MacCrimmon and Twongo 1980; Wallace and Aasjord 1984), inflation of the gas bladder (Heming et al. 1982), attainment of maximum alevin wet weight (Heming 1982), or disappearance of the visible yolk sac (Atkins 1905; White 1915).

In our experiments the first feeding tests were usually conducted several days before the alevins started feeding. At this age the alevins hid under the gravel, showing a photonegative behaviour. We did not study the behaviour of the alevins in detail, but observed that the alevins had food in their intestines a long time before the yolk was exhausted. Usually 5–7 d elapsed between 10% and 90% alevin feeding.

Some studies are available on the development time to 50% emergence in Atlantic salmon (Dill 1977; Gunnes 1979; Brännäs 1987). Comparing our results on time at 50% feeding with those on time at 50% emergence, indications were found that, on the average, Atlantic salmon alevins fed before emergence. This is in accordance with observations by Gustafson-Marjanen and Dowse (1983), on newly emerged alevins which had easy access to Simulium larvae. All eight fish examined "... had clearly fed well on them before emergence...". Stuart (1953) and Field-Dodgson (1988) report similar observations. Dill (1977), in his studies on behaviour of Atlantic salmon, observed that mean starting times of snapping and darting occurred soon after the mean emergence age.

The curves describing time to 50% feeding in brown trout and in Atlantic salmon are given in Fig. 3, along with corresponding data for Arctic char (Wallace and Aasjord 1984). These are the only three anadromous salmonids naturally occurring in Norwegian salmon rivers. Above about 8°C, the development time to 50% feeding is about the same for all three species. However, at lower temperatures clear differences are found. Atlantic salmon alevins need more time to reach the stage of initial feeding at low temperatures than do Arctic char, while brown trout are intermediate. The results are in accordance with the optimum temperature range for all three species (Elliott 1981; Wandsvik and Jobling 1982), as well as with their geographic distribution. The "optimum temperature range," defined as the range over which feeding occurs and there are no external signs of abnormal behavior, is 3–16, 4–19, and 6–20 °C for Arctic char, brown trout, and Atlantic salmon, respectively (Elliott 1981; Wandsvik and Jobling 1982). The optimum temperature for growth is 11–14 °C for Arctic char (Jobling 1983; Jensen 1985), 13°C for brown trout (Elliott 1975) and 16–17 °C for Atlantic salmon (Siginevich 1967; Dwyer and Piper 1987). While Arctic char feed and grow at temperatures as low as 3°C (Wandsvik and Jobling 1982), and brown trout at 4°C (Elliott 1975), Atlantic salmon move from riffles to pools at temperatures below 7°C and reduce or stop feeding (Allen 1940, 1941; Gardiner and Geddes 1980; Jensen and Johnsen 1986). Arctic char has the most northerly distribution, and is the only fish species found in freshwater as far north as Svalbard (Dahl 1926; Gullestad 1975). The natural southern boarder in Europe for sea-run Arctic char is at 65°N in Norway (Jensen 1981), while sea-run brown trout are found as far south as the Bay of Biscaya (Frost and Brown 1967). Atlantic salmon are found south to the Douro River in Portugal at 41°N (MacCrimmon and Gots 1979).

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Activity, Respiration, and Excretion of Ammonia by Atlantic Salmon (*Salmo salar*) Smolt and Postsmolt

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Spontaneous activity, oxygen consumption, and excretion of ammonia by juvenile Atlantic salmon (*Salmo salar*) were measured over 17 wk as the appearance of the fish changed from early smolt to smolt and then postsmolt. A substantial change in routine oxygen consumption from 66 to 148 $mL \cdot kg^{-1} \cdot h^{-1}$ was primarily correlated with the increase in activity. An initial increase in ammonia excretion from about 5 to about 14 $mL \cdot kg^{-1} \cdot h^{-1}$ was largely correlated with the decline in condition factor from 0.99 to 0.79 suggesting that increased metabolic needs caused by the increased activity were not being met by the amount of food ingested. This is supported by the secondary increase in condition factor (C.F. = 0.93) and decrease in ammonia excretion (to about 7 $mg \cdot kg^{-1} \cdot h^{-1}$) that occurred after the meal size was increased.

L'activité spontanée, la consommation d'oxygène et l'excrétion d'ammoniac par le jeune saumon de l'Atlantique (*Salmo salar*) ont été mesurés pendant 17 sem à mesure que le poisson changeait d'aspect, passant de l'aspect de jeune smolt, de smolt puis de post-smolt. Une augmentation importante de la consommation habituelle d'oxygène de 66 à 148 $mL \cdot kg^{-1} \cdot h^{-1}$ était principalement corrélée à l'augmentation de l'activité. Une augmentation initiale de l'excrétion d'ammoniac de 5 à environ 14 $mL \cdot kg^{-1} \cdot h^{-1}$ était largement corrélée à la diminution du coefficient de condition de 0,99 à 0,79, ce qui laisse supposer que la quantité d'aliments ingérés ne suffit pas à combler les besoins métaboliques plus grands provenant de l'activité accrue. Cette hypothèse est appuyée par l'augmentation secondaire du coefficient de condition (0,93) et par la diminution de l'excrétion d'ammoniac (à environ 7 $mg \cdot kg^{-1} \cdot h^{-1}$) observée après une augmentation de la quantité d'aliments disponibles.

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Parr–smolt transformation of salmonids involves changes in morphology, biochemistry, physiology, and behaviour (Wedemeyer et al. 1980). The characteristic silvering of the skin represents the deposition of considerable amounts of nitrogen as guanine and hypoxanthine (Johnston and Eales 1967). The slimmer appearance of the smolt indicated by the decrease in the condition factor suggests, in part, a change in body proportions caused by the differential growth which occurs during smoltification.

An increased growth rate of smolt compared with parr (Saunders and Henderson 1970) is correlated with increased pituitary somatotroph activity (Kamourdjian et al. 1976) and increased concentrations of plasma growth hormone (Sweeting et al. 1985). Levels of plasma thyroid hormone are also increased during smoltification (Simpson and Thorpe 1976; Kristinsson et al. 1985; McCormick et al. 1987) and may contribute to the increased growth rate. All of these factors would be expected to produce a state of positive nitrogen balance.

Previous work on the metabolic origin of nitrogenous excretory products indicates that ammonia is the principal end product of amino acid catabolism in salmonids while urea results primarily from purine degradation (Brett and Zala 1975; Walton and Cowey 1982; Van Waarde 1983). Consequently, the observation that ammonia excretion increased during smoltification did not appear to be consistent with smoltification being an anabolic process.

Alternatively, the lower condition factor commonly associated with smoltification could indicate the depletion of body reserves. A decrease in body lipid (Farmer et al. 1978) and a decrease in liver glycogen (Wendt and Saunders 1973) have been observed at smoltification. This could indicate that there has been a change in the energy balance of the fish which could be caused by several factors such as a change in food intake, standard metabolic rate, or activity.

We measured changes in activity, ammonia excretion, and oxygen consumption of juvenile Atlantic salmon (*Salmo salar*) during the final period of smoltification (April–May) and during a 2-mo further retention in freshwater (June–July) to determine whether the changes in oxygen consumption and ammonia excretion were caused by a change in the standard metabolism associated with the smoltification process.

Materials and Methods

Atlantic salmon from the Cobequid Fish Culture Station, Cobequid, N.S. were transported to the St. Andrews Biological Station in December and placed in cylindrical fibreglass tanks containing approximately 390 L of dechlorinated water from Chamcook Lake. Water was supplied at a rate of 7 $L \cdot min^{-1}$.

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TABLE 1. Diet formulation.

Component	Food (%·g)	Protein(g)	Carbohydrate(g)	Lipid(g)
Herring meal	60.1	47.0	—	6.31
Herring oil	3.84	—	—	3.84
Cod liver oil	2.81	—	—	2.81
Corn oil	3.74	—	—	3.74
Dextrin	16.7	—	16.7	—
Mineral mix[a]	1.87	—	—	—
Vitamin mix[b]	1.54	—	—	—
C.M.C.[c]	9.40	—	—	—
Total	100	47.0	16.7	16.7
Ash	8.59	—	—	—
Calories[d]	5170	—	—	—

[a]Zeitoun et al. 1973.
[b]Vitamin pack designed for Atlantic salmon (A.M. Sutterlin, pers. comm.).
[c]C.M.C. = carboxy-methyl-cellulose.
[d]Means of duplicate estimation by Bomb Calorimetry carried out by C. Hall.

Tanks were aereated and provided with small submersible pumps which produced a consistent current near the surface of about 1.0 body length·s^{-1} when measured at the periphery of the tank where the fish were typically located.

By early March the fish had been acclimated to 13.7°C. From April 1 to June 30 the temperature was held at 13.6°C (SD = 0.39°C). At this time, because of the unusually warm summer we were unable to maintain the temperature which gradually rose and then restabilized at a mean of 16.0°C (SD = 0.35°C) in July.

Fish were fed a moist pellet (Table 1). The meal size, calculated on the basis of dry weight food per gram dry weight of fish was initially 3.5% but had to be increased after June 30, and reached 8.6% by July. Normally all food was eaten.

Photoperiod simulated the normal seasonal increase in day length (15 min·6 d^{-1}) but was retarded (by approximately 2.5 mo relative to natural day length with an 8.5-h day being initiated on March 4) in an attempt to delay the final stages of smoltification. Subsequently, we saw no reason to think that this had any effect, probably because smoltification was relatively advanced when the procedure was started.

At weekly intervals, fish of about 16 cm (or 35 g) were fasted for 48 h, anesthetized with tertiary-amyl alcohol, weighed, measured, and placed in each of three static volume respirometers (22-L volume, Beamish and Mookherjii 1964) which were maintained at 14°C (SD = 0.02) throughout the study.

The three fish placed in each respirometer were matched for size and appearance (silvering, etc.), but no other conscious selection occurred. Measurements began after 24 h when the fish had presumably recovered from handling. On each day for the next 3 or 4 d at 08:15, 11:15, and 14:15, oxygen consumption was determined over a 2.5-h period using the Winkler method. Activity was measured using the method of Beamish and Mookherjii (1964). Each respirometer was surrounded by a water bath precisely maintained at a temperature slightly below 14°C (about 1–2°C). The activity meter consisted of a small heater and timer which maintained the respirometer at 14°C by working against the cooling effect of the external water bath. The system was adjusted and calibrated so that the heaters had to operate for a specific fraction of the time (approximately 50%) to maintain 14°C. The stirring caused by the activity of the fish increased the cooling rate and the subsequent heater operating time (Withey and Saunders 1973).

$$\% \text{ Relative activity} = \frac{\text{Heater operating time in presence of fish}}{\text{Heater operating time without fish}} \times 100.$$

Ammonia excreted into the water was measured with the phenate-hypochlorite method (Kaplan 1969). On some occasions this procedure (applied to subsamples of water which had been treated with a buffered urease to convert urea to ammonia) was used to measure urea.

We also calculated ammonia quotients;

(A.Q. = ammonia excreted·oxygen consumed^{-1}·100%,

(Kutty 1972; Van Waarde 1983) and condition factor (C.F. = weight·length^{-3}·100%). Because these and activity values were ratios they were routinely subjected to the arcsine transformation (Zarr 1974). Other standard transformations were applied as needed, after the examination of the residuals from a preliminary analysis. The SAS (Helwig and Council 1979) and BMDC (Dixon and Brown 1979) computer packages were used to analyze the data using a simple correlation procedure (SAS-Corr) and a multiple regression procedure (BMDP2R). Regression of each dependent variable was carried out using the following as independent variables as appropriate:

Activity = Spontaneous activity of fish in the respirometer measured as % relative activity.
Ammonia = Ammonia excretion measured in millilitres per kilogram per hour.
Condition = Mean condition factor of fish determined over measurement period.
Day (or week) = Time since the beginning of the study.
Diurnal = Time period during which the measurement was made No. 1 (08:15–10:45), No. 2 (11:15–13:45), or No. 3 (14:15–16:45).
Fast = Duration of fasting (days).
Length = Mean length of fish over measurement period.
Meal = Amount of food fed per gram of fish per day prior to respirometry.
Oxygen = Oxygen consumption measured in millilitres per kilogram per hour.
Oxcon = Mean oxygen concentration (millilitres oxygen per litre) in respirometer during the measurement period.
Resp = Identification of individual respirometer (1, 2, or 3); used to assess potential differences attributable to a specific respirometer.
Temp = Temperature (degrees Celsius) in culture tanks prior to respirometry.

Individual variables were assumed to have a significant effect if they reached a level of $P < 0.05$.

Results and Discussion

During the study the appearance of the fish changed from that of early smolt with residual parr marks to that of fully silvered smolt with dark fin margins. By early May the black margins had become strikingly evident but by July they had faded. The fish became typically thinner as the smolt coloring developed with the C.F. (Fig. 1a) declining from 0.99 in April to a low of 0.79 in June and then recovering to 0.93 by the end of July.

To facilitate comparison with existing studies all the data for each week were averaged and plotted (Fig. 1b–d). Significant

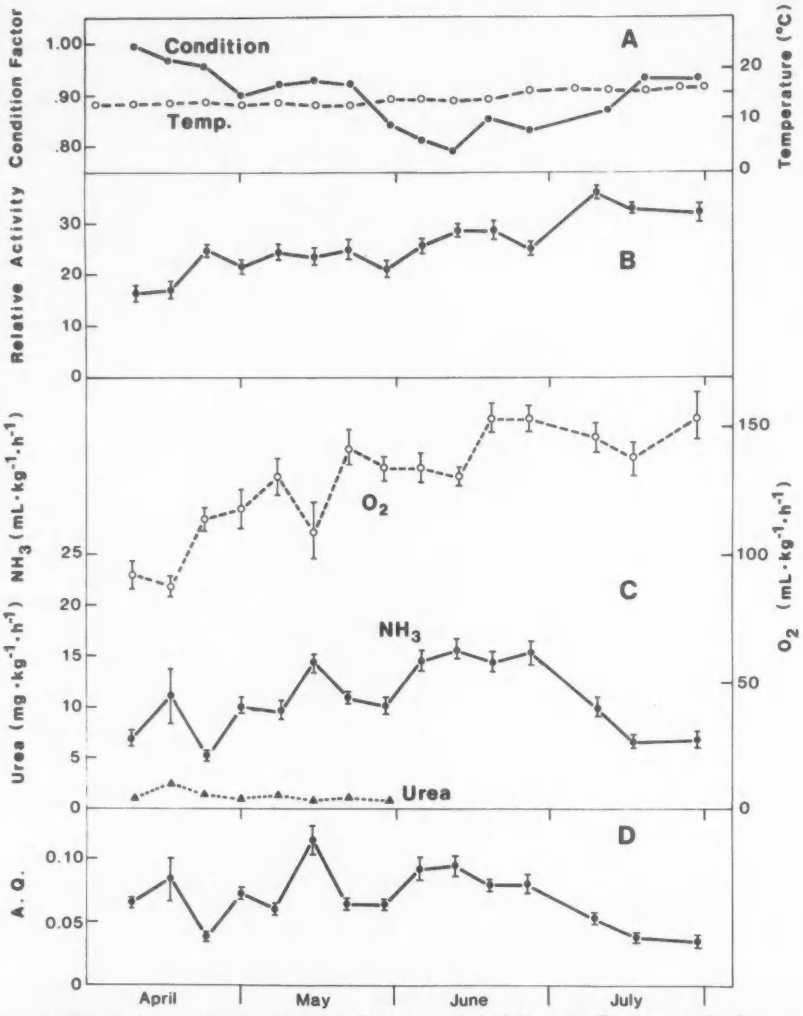

FIG. 1. Changes in several parameters over the 4-mo period of the study. For most weeks the means represent from 27 to 36 values. (Usually observations were made, using three respirometers, at three times of the day, on each of 3 d in the week. Occasionally measurements were made on only 2 or 4 d.) Bars represent ± 1SE of the mean, except for the condition factor. Since this was the mean of only three observations SE's were not calculated. (A) Changes in condition factor (C.F.) and temperature, (B) changes in activity (expressed a percent relative to a previously established baseline), (C) changes in oxygen consumption and ammonia excretion ($mL \cdot kg^{-1} \cdot h^{-1}$) and urea excretion ($mg \cdot kg^{-1} \cdot h^{-1}$). (D) Changes in ammonia quotient (A.Q.). Lines connecting points are provided to indicate trends.

correlations (at $P = 0.0001$) existed between activity and time ($R = 0.55$), routine metabolism and time ($R = 0.53$), and ammonia excretion and time ($R = 0.26$) indicating that changes were occurring in all three variables during the study. However, significant correlations (at $P = 0.0001$) between oxygen consumption and both ammonia excretion ($R = 0.30$) and activity ($R = 0.59$) suggested that some of the correlations with time might be spurious. Since the results for each week were from the same fish we had planned to use the pooled data to calculate a regression between activity and oxygen consumption and then to estimate the standard metabolic rate for that week. Because of the probability of spurious correlations and because significant differences other than those related to activity existed among the results obtained at different times of the day, as well as among the results obtained from consecutive days, this procedure was felt to be invalid.

To sort out the complex relationships, multiple regression analysis was used to determine which of the independent variables were significantly influencing each of the dependent variables; oxygen consumption, activity, and ammonia excretion. This procedure had the added advantage of providing an estimate of the magnitude of the effect of each independent variable (partial regression coefficient). Since this analysis has its own limitations and does not establish cause and effect, it was necessary to consider the biological validity of each significant effect. Virtually all of the "correlations" were in fact consis-

tent or compatible with what is known about the physiology of juvenile salmon. As will be seen, the number and magnitude of the few exceptions were minor.

Analysis of the data for spontaneous activity (Fig. 1b) by stepwise multiple regression produced the equation (standardized form); Activity (arcsin %) = 0.0 + 0.57 $\text{Weeks}_{(0.33)} - 0.51\ \text{Temp}_{(0.03)} - 0.13\ \text{Diurnal}_{(0.02)} + 0.51\ \text{Meal size}_{(0.02)} + 0.14\ \text{Length}^2_{(0.02)} + 0.09\ \text{Fast}_{(0.02)}$. The multiple regression coefficient, $R = 0.65$. (Subscript values in parentheses represent the partial coefficient or the increase in the multiple regression coefficient ("explained variation") contributed by each variable).

Activity not only increased during the study but also with the size of the fish, meal size, and with the duration of the fast; but decreased during the day and with an increase in the culture temperature. This increase in the spontaneous activity is probably a direct consequence of smoltification (Saunders and Henderson 1970; Fontaine and Marchelidon 1971).

The multiple regression equation for metabolic rate (Fig. 1c) was; Oxygen consumption = 0.0 + 0.37 $\text{arcsine Activity}_{(0.34)} - 0.27\ \text{arcsine Condition}^2_{(0.12)} - 0.28\ \text{Fast}^2_{(0.08)} - 0.26\ \text{Diurnal}_{(0.06)} + 0.17\ \log \text{Weeks}_{(0.02)} + 0.14\ \log \text{Length}_{(0.01)}$. The multiple regression coefficient, $R = 0.80$.

Oxygen consumption increased directly with activity, size, time elapsed since the beginning of the study, and as condition declined, but decreased during the day and with the duration of fasting. In this case activity, condition factor, duration of fast, and time of day contributed substantially.

During our study routine oxygen consumption (Fry 1957) at 14°C increased from about 66–148 $\text{mL}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ (mean weight of all fish used was 39 g; SD = 7.93). Baraduc and Fontaine (1955) reported routine values for oxygen consumption measured at 7.4–8.3°C of 73 $\text{mL}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ for Atlantic salmon parr (38 g mean weight) and 97 $\text{mL}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ for smolt (49 g mean weight). Brett and Zala (1975) reported routine values of 66.4 $\text{mL}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ for sockeye salmon (*Oncorhynchus nerka*) fingerlings (mean weight = 29 g) at 15°C.

Our regression analysis correlates much of the increase in oxygen consumption during our study with the increase in activity. The standard metabolic rate (Fry 1957) at 14°C calculated by applying our regression equation to a 15 cm (39 g) fish, C.F. = 1.00, measured at the beginning of the study in observation period 1 (morning) with zero fasting and zero activity was 77 $\text{mL}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$. Withey (1972) reported standard metabolic rates for post smolts at 15°C to be 69.7 $\text{mL}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ (mean weight = 194 g).

In addition to changes in oxygen use caused by the increased activity, there was an additional small increase in oxygen consumption during the study which seemed to be independent of activity, suggesting that smolt do have a slightly higher standard metabolism than parr. The size of this increase is slight and much less than the substantial increase (73–97 $\text{mL}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$) reported by Baraduc and Fontaine (1955). However, their results appear to be for routine oxygen consumption and do not allow for the substantial increase in activity that occurs in association with smoltification. Since our study did not begin until April when smoltification was already in progress, our results probably do not indicate the full magnitude of the change in oxygen consumption associated with smoltification. It also is possible that the change is related to some other parameter such as season (Beamish 1964b) or summer photoperiod (Withey and Saunders 1973) and not to smoltification directly.

Higgins (1985) showed that smolt not only have greater rates of oxygen consumption but also the slope of the weight–metabolism regression line for smolt was greater than that for parr. This suggests that the differences in metabolism between parr and smolt are qualitative as well as quantitative. A qualitative change in metabolic processes such as described by Higgins (1985) could provide an explanation for our unusual observation that the weight specific metabolic rate appears to increase with size because our observations began with presmolt, continued with smolt and ended with postsmolt. Brett's (1965) observation that the size–metabolism relationship for Pacific salmon increases with activity offers another possible explanation because activity and size both increased during the study.

Although statistically significant, the effect of several of the independent variables was minor in that they contributed little (partial regression coefficient of about 0.02) to the change in the dependent variable and hence to the multiple regression coefficient. Some relationships such as the increase in oxygen use as C.F. fell, or like the increase in activity with length or meal size, may well be biologically meaningful. They may also be statistical artifacts resulting from the fact that many of the variables are not truly independent, but are covariates. For example, condition factor, ration, and length all increased over the duration of the study and to some degree are correlated with time and therefore the process of smoltification as well as the associated increase in activity and metabolism. However, the results are generally biologically realistic, the residuals are normally distributed, and pairwise correlations between the variables showed correlation coefficients less than 0.7–0.8. Therefore, we felt justified in concluding that the possible covariate nature of the variables was unlikely to have affected the analysis in a substantial way (Slinker and Glantz 1985).

The multiple regression equation for ammonia excretion (Fig. 1c) was; Ammonia = 0.0–0.41 $\log \text{arcsine Condition}_{(0.32)} - 0.48\ \text{Meal size}_{(0.03)} + 0.37\ \text{Days}_{(0.03)} - 0.16\ \text{Fast}_{(0.02)}$. The multiple regression coefficient, $R = 0.63$.

Effectively, ammonia excretion increased during the study and as C.F. declined but fell during the period of fasting and when the meal size was increased. C.F. was the only variable to have a substantial effect.

The amount of ammonia (5.9–15.6 $\text{mL}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$) and urea (1.0–2.4 $\text{mg}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$) excreted by Atlantic salmon smolt were comparable with values for ammonia (6.2 $\text{mL}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$) and urea (2.2 $\text{mg}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$) reported for fingerling sockeye (Brett and Zala 1975). During our study the substantial changes in ammonia excretion, the primary byproduct of protein catabolism seemed primarily related to nutritional state. Ammonia excretion increased as temperature (and energy requirements) increased while at the same time C.F. fell (and whole body lipid reserves decreased, A. J. Wiggs, unpubl. data). Later, with an increase in meal size, ammonia excretion declined as C.F. improved.

To further investigate the relationship between oxygen consumption and ammonia excretion, the ammonia quotient (Fig. 1d) was calculated, yielding the multiple regression equation; A.Q. = 0.0 –0.30 $\text{arcsine Condition}_{(0.11)} - 0.31\ \text{arcsine Activity}_{(0.10)} - 0.40\ \text{Temp.}_{(0.02)} + 0.32\ \text{Weeks}_{(0.02)}$. The multiple regression coefficient, $R = 0.50$.

This suggests that the oxidative catabolism of protein (A.Q. increased through the study yet declined with increasing activity, temperature and an improvement in C.F., only activity and C.F. having substantial effects.

Because protein catabolism seems to play a major role in satisfying the energy requirements of fish (Van Waarde 1983), we expected to find a significant correlation between ammonia excretion and metabolic rate or activity. Neither could be demonstrated directly. In fact the decrease in A.Q. with increased activity suggested that protein use did not increase proportionately with activity. Similar results led Kutty (1981) to suggest that protein might be used at relatively constant rates to meet basal energy needs with other substrates being used to meet the increased energy needs resulting from activity (Van Waarde 1983). The results of Kutty (1972); Driedzic and Hochachka (1978); and Holeton et al. (1983), show an increase in ammonia excretion with activity. A. J. Wiggs (unpubl. data) measured a 1.6-fold increase in ammonia excretion when young salmon were forced to swim at 2 body lengths·s^{-1} compared with the excretion by the same individuals under routine conditions. It is not clear whether the differences are attributable to the differences between metabolic processes associated with spontaneous (burst) activity and sustained activity (Kutty 1981), the stage of smoltification or some other factor.

The suggestion that ammonia excretion resulted from the oxidative catabolism of protein during the early part of the study is consistent with the increase in A.Q. (from 0.06 to 0.14). Kutty (1981) estimated that an A.Q. of about 0.33 would result from the aerobic catabolism of protein alone. Our values were lower and presumably indicate the oxidation of other fuels with protein. A.Q. values greater than 0.33 are usually associated with hypoxia (Kutty 1978) and were not observed in our study. There were no demonstrable correlations between any of the measured variables and the oxygen concentration in the respirometers. The significance of the small increase in ammonia excretion with time (stage of smoltification) is not clear from our work.

The decrease in oxygen consumption and ammonia excretion that continued after the fish were placed in the respirometer suggests that a 2-d fast was insufficient to allow metabolism to fall to a basal state. Brett and Zala (1975) found that the effect of digestion on the routine metabolism of sockeye fry was limited to about 18 h at 15°C. Beamish (1964a) found that about 3 d were required for the standard metabolism of brook trout (*Salvelinus fontinalis*) to stabilize at 10°C while Dickson and Kramer (1971) saw changes in oxygen consumption for up to 9 d of fasting in rainbow trout (*Salmo gairdneri*).

In our study the small increase in activity that occurred over 3–5 d in the respirometer did not appear to change oxygen consumption. Probably the rather larger decrease in oxygen consumption associated with the onset of fasting masked a smaller effect associated with activity. Similarily it is not clear whether the decrease in oxygen consumption during the day is a postprandial effect or the result of a daily rhythm. Brett and Zala (1975) observed a peak oxygen consumption at the normal meal time with a subsequent decline during the day.

A relatively small amount of the variation in the ammonia excretion could be correlated with the independent variables suggesting that other major unidentified variables exist. The lack of a direct measure of the stage of smoltification is a major limitation.

In contrast with the variability in ammonia excretion our data indicate a rather low and fairly consistent level of urea excretion. Urea production in salmonids primarily originates from purine catabolism (Van Waarde 1983). Since the silvering associated with smoltification results from purine synthesis and deposition (Johnston and Eales 1967) a low level of urea excretion seems reasonable.

In summary, our results indicate that the primary increase in oxygen consumption during the later stage of smoltification is related to the increased activity of smolt. The resulting increased metabolic demand appears to have resulted in the depletion of lipid reserves (decreased C.F.) and led to an increased protein catabolism and consequently increased excretion of ammonia.

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Adaptive Changes in Hematologic and Plasma Chemical Constituents in Captive Beluga Whales, *Delphinapterus leucas*

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St. Aubin, D. J., and J. R. Geraci. 1989. Adaptive changes in hematologic and plasma chemical constituents in beluga whales, *Delphinapterus leucas*. Can. J. Fish. Aquat. Sci. 46: 796–803.

Forty-two beluga whales, *Delphinapterus leucas*, were captured in the Seal and Churchill River estuaries in western Hudson Bay during July, 1985 and 1987. Blood samples were drawn from each whale, and analyzed for cellular elements, electrolytes, metabolites, enzymes, proteins, and adrenocortical hormones. Most of the whales were released immediately after sampling; six were maintained in holding facilities for 10 wk during 1985. Blood samples drawn during the early stages of acclimation to captivity, and at irregular intervals thereafter, revealed the variety of metabolic adjustments that accompanied the transition to captivity. The stress and exertion of capture resulted in increased levels of aldosterone, cortisol, glucose, iron, potassium, and the enzymes creatine kinase, aspartate aminotransferase, alanine aminotransferase, and γ-glutamyltranspeptidase. Acute changes in leucocytes included lymphopenia, eosinopenia, and mild neutrophilia. Most of these indices normalized within the first week in captivity. Progressive changes were noted in triglycerides and creatinine, reflecting the whales' altered diet and caloric intake. A steady decline in red cell mass was indicative of reduced demands on oxygen carrying capacity, and provided a clue to the significance of low hematocrits reported for whales sampled after several weeks in shallow estuaries.

Quarante deux bélugas, *Delphinapterus leucas*, ont été capturés dans les estuaires des rivières Churchill et Seal dans l'ouest de la baie d'Hudson en juillet 1985 et 1987. On a prélevé des échantillons sanguins de chaque baleine et analysé les éléments cellulaires, les électrolytes, les métabolites, les enzymes, les protéines et les hormones corticosurrénales. La plupart des baleines ont été libérées immédiatement après la prise de sang; six d'entre elles ont été maintenues en captivité pendant 10 sem en 1985. Les échantillons de sang prélevés au cours des premiers stades de l'acclimatation à la captivité et à intervalles réguliers par la suite ont révélé la variété des adaptations métaboliques qui ont accompagné la transition à la captivité. Le stress et l'opération de capture ont augmenté les concentrations d'aldostérone, de cortisol, de glucose, de fer, de potassium, et des enzymes créatine kinase, aspartate aminotransférase, alanine aminotransférase, et γ-glutamyltranspeptidase. On a observé des changements aigus de la formule leucocytaire, par exemple une lymphopénie, une éosinopénie et une légère neutrophilie. La plupart de ces indicateurs sont revenus à la normale dans la première semaine de captivité. On a observé des changements graduels dans la concentration des triglycérides et de la créatinine, causés par la modification du régime et de l'apport calorique. La diminution constante de la masse des globules roupes indiquait une demande réduite de la capacité de transporter l'oxygène et permettait d'expliquer les faibles hématocrites signalés dans les échantillons de sang prélevé sur des baleines ayant séjourné plusieurs semaines dans des estuaires peu profonds.

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In 1967, Canadian government biologists captured, marked, and released a number of beluga whales, *Delphinapterus leucas*, in western Hudson Bay (Sergeant and Brodie 1969). Blood samples were collected from 17 of the whales, for comparison with captive specimens (Geraci et al. 1968a, 1968b). Differences in several hematologic parameters signalled that the whales had made physiological adjustments to captivity, though at the time it was not possible to monitor the progress of these adaptations.

Nearly 20 yr later, a similar program afforded an opportunity to sample the same population of animals, and chart the dynamics of hematologic and plasma chemical constituents in six whales transported and retained in captivity for 10 wk. To the baseline data available for these and other cetaceans (Ridgway et al. 1970; MacNeill 1975; Cornell 1983; Medway and Geraci 1986), we add a profile of clinically useful blood analyses and focus on the constituents that are the most sensitive to environmental influences. The findings provide us with a better understanding of metabolic changes that accompany the transition to captivity.

Materials and Methods

In early July 1985, 24 subadult beluga whales (18 males (M), 6 females (F)) were captured in the Seal River estuary (59°04′N, 94°48′W) in western Hudson Bay. In mid-July 1987, 18 whales (16 M, 2 F) were captured in the nearby Churchill River (58°37′N, 94°07′W). The whales ranged in length from 246–381 cm ($\bar{x} \pm SD = 285 \pm 33$ cm); large adults and females with calves were purposely avoided. The duration of the approach and capture was typically less than 30 min. Each whale was measured and sexed, and blood samples were col-

lected. Thirty-six of the whales were released immediately; six (3 M, 3 F) of those captured in 1985 were placed on stretchers and transported 15 km to a field camp, where they were maintained for 10 wk in two 8-m diameter pools containing 3.8×10^4 L of seawater renewed daily from Hudson Bay. The animals were offered Pacific herring, *Clupea harengus pallasi*, and began feeding within 7 d after capture. Their diet was supplemented with vitamins, and provided an average of 40 $kcal \cdot kg^{-1} \cdot d^{-1}$, though consumption varied from day to day. Two of the whales maintained or increased their weight on this diet; the other four lost 25–50 kg.

Blood samples were collected from four of the whales following the 2–3 h transfer from the capture site to the holding facilities, and from all six captives at irregular intervals during the 10 wk study. Blood from the tail flukes was drawn into vacuum tubes containing heparin or ethylene-diamine-tetra-acetic acid for plasma chemical and hematologic analyses, respectively. Hematology samples collected at the capture site were held on ice for up to 12 h before processing; those from captive animals were processed within 1 h.

Hematology

Samples collected at capture were analyzed at the Churchill Health Center, Churchill, Manitoba. Red blood cell counts, hemoglobin (Hb), mean corpuscular volume (MCV), mean corpuscular hemoglobin (MCH), and mean corpuscular hemoglobin concentration (MCHC) were determined using a CC-130 automated particle counter in 1985 and a T660 counter in 1987 (Western Scientific, Vancouver, B.C.).

In the field camp, total leucocyte and eosinophil counts were performed in duplicate using Unopette systems (Becton-Dickinson, Rutherford, NJ) and a Neubaur hematocytometer (American Optical, Buffalo, NY). White blood cell (WBC) distribution was determined from counts of 200 cells in smears stained with Wright's. Packed cell volume (PCV) was determined by the microhematocrit method, and Hb using a Spencer hemoglobinometer (American Optical). To validate the precision of the manual methods, 10 determinations were made on a sample from each of two whales. Average coefficients of variation were 1.3% for PCV, 3.7% for Hb, 17.3% for total eosinophils and 18.0% for WBC.

Plasma Chemistry

Plasma harvested after centrifugation was stored frozen for up to 2 mo. Electrolytes and metabolites were determined on a multichannel, automated Parallel Analyzer (American Monitor Corp., Indianapolis, IN) and enzymes were measured using a SMAC System (Technicon Instrument Corp., Tarrytown, NY), according to the manufacturers' prescribed metholologies (Table 1). Enzyme activity is reported in international units (U); one unit represents the conversion of 1 mole of substrate per second. Aliquots of a pooled sample of beluga plasma were randomly included among the study samples to verify that coefficients of variation between and within batches of analyses were less than 5%.

Plasma proteins were separated by electrophoresis on agar gel with barbital buffer at pH 8.6. Protein fractions were stained with amido black, and quantitatively analysed using a Clifford densitometer (Corning Ltd., Palo Alto, CA).

TABLE 1. Methodologies for automated analyses of plasma chemical constituents in beluga whales.

Constituent	Method
Metabolites and Electrolytes[a]	
Calcium	0-cresolphthalien complexone dye (CPC)
Chloride	2,4,6-tripyridyl-S-triazine dye (TPTZ)
Sodium	Atomic emission
Potassium	Atomic emission
Phosphorus	Polyvinylpyrrolidone dye (PVP)
Urea	Phthalaldehyde and 8-(4-amino-1 -1 methylbutyl-amino)-6-methoxyquinoline
Uric acid	Phosphotungstate reduction
Glucose	Glucose oxidase — peroxidose
Creatinine	Picrate complex
Cholesterol	Cholesterol ester hydroxylase — cholesterol oxidase
Iron	Ferrous ion-chromophore complex
Protein	Biuret reaction
Triglycerides	Lipase digestion, glycerokinase, glycerol-3-phosphate dehydrogenase, NAD reduction coupled to Fe reduction, chromophore production
Enzymes[b]	
Creatine kinase (CK)	ADP phosphorylation, coupled to hexokinase and glucose-6-phosphate reduction of NADP
Alkaline phosphatase (AP)	Nitrophenyl phosphate hydrolysis
alanine aminotransferase (AlAT)	Transamination coupled to NADH oxidization by lactate dehydrogenase
Aspartate aminotransferase (AsAT)	Transamination coupled to NADH oxidization by malate dehydrogenase
Lactate dehydrogenase (LDH)	Pyruvate reduction, NADH oxidization
γ-glutamyltranspeptidase (GGT)	Formation of nitroaniline dye

[a]Metabolites and electrolyes according to American Monitor Corp., Indianapolis, IN.
[b]Enzymes according to Technicon Instrument Corp., Tarrytown, NY.

TABLE 2. Hematologic and plasma chemical constituents in free-ranging beluga whales sampled within 1 h of capture.

Constituent	Units	N	$\bar{X}$	SD	Range	Median
Red blood cells	$10^{12} \cdot L^{-1}$	40	3.61	0.28	3.0–4.1	3.64
Hematocrit	$L \cdot L^{-1}$	42	0.59	0.04	0.52–0.66	0.58
Hemoglobin	$g \cdot L^{-1}$	42	223	16	180–260	220
Mean corpuscular volume	fL	40	164	10	142–179	175
Mean corpuscular hemoglobin	pg	40	61.7	4.8	52.5–75	62.0
Mean corpuscular hemoglobin concentration	$g \cdot L^{-1}$	42	378	23	339–448	375
White blood cells*	$10^9 \cdot L^{-1}$	40	10.7	2.7	5.7–16.9	10.8
Mature neutrophils*	$10^9 \cdot L^{-1}$	40	4.0	1.3	2.4–7.8	3.7
Immature neutrophils	$10^9 \cdot L^{-1}$	40	0.1	0.1	0.0–0.7	0.1
Lymphocytes*	$10^9 \cdot L^{-1}$	40	3.5	1.3	0.9–6.9	3.6
Monocytes	$10^9 \cdot L^{-1}$	40	0.5	0.2	0.1–0.9	0.4
Basophils	$10^9 \cdot L^{-1}$	40	0.1	0.1	0.0–0.4	0.1
Eosinophils	$10^9 \cdot L^{-1}$	40	2.5	1.2	1.0–6.7	2.5
Sodium	$mmol \cdot L^{-1}$	40	163	9	134–182	165
Potassium	$mmol \cdot L^{-1}$	40	5.1	1.0	3.4–8.2	5.0
Chloride	$mmol \cdot L^{-1}$	40	114	6	101–132	114
Calcium	$mmol \cdot L^{-1}$	40	2.5	0.3	1.9–2.9	2.5
Phosphorus	$mmol \cdot L^{-1}$	40	2.7	0.3	2.0–3.4	2.8
Iron	$\mu mol \cdot L^{-1}$	32	45	16	25–87	42
Glucose	$mmol \cdot L^{-1}$	40	6.0	1.1	4.1–9.1	5.8
Cholesterol	$mmol \cdot L^{-1}$	40	3.3	0.9	1.3–5.4	3.4
Triglycerides	$g \cdot L^{-1}$	35	1.63	0.34	0.58–2.47	1.62
Urea	$mmol \cdot L^{-1}$	40	20.0	3.3	13.1–30.9	20.0
Uric acid	$\mu mol \cdot L^{-1}$	40	12	13	0–45	10
Creatinine	$\mu mol \cdot L^{-1}$	17	234	57	137–337	218
Cortisol	$nmol \cdot L^{-1}$	41	90	43	18–196	91
Aldosterone	$pmol \cdot L^{-1}$	37	224	237	40–1147	52
Creatine kinase	$U \cdot L^{-1}$	39	218	87	44–499	217
Alkaline phosphatase	$U \cdot L^{-1}$	33	36	131	54–573	229
Aspartate aminotransferase	$U \cdot L^{-1}$	28	109	46	55–231	100
Alanine aminotransferase	$U \cdot L^{-1}$	30	35	41	0–167	24
Lactate dehydrogenase	$U \cdot L^{-1}$	23	355	99	216–574	341
γ-glutamyltranspeptidase	$U \cdot L^{-1}$	13	6	7	0–20	5
Total protein	$g \cdot L^{-1}$	21	83	6	71–98	80
Albumin/globulin	$g \cdot L^{-1}$	21	1.1	0.2	0.8–1.5	1.1
Albumin	$g \cdot L^{-1}$	21	43	4	35–52	43
Globulin	$g \cdot L^{-1}$	21	40	4	32–48	40
Alpha 1	$g \cdot L^{-1}$	21	3	<1	2–4	3
Alpha 2	$g \cdot L^{-1}$	21	8	1	6–11	8
Beta 1	$g \cdot L^{-1}$	21	6	2	3–13	6
Beta 2	$g \cdot L^{-1}$	21	5	2	3–11	5
Gamma	$g \cdot L^{-1}$	21	17	3	12–22	17

*Analysis using Student *t*-test reveals a significant difference in results between sample years. Refer to text and Table 3.

TABLE 3. Leucocyte counts (10^9 cells$\cdot L^{-1}$) in 24 belugas captured in 1985 and 16 in 1987. All values in 1987 were significantly ($p < 0.01$) higher than in 1985.

Cell type	Year	$\bar{x} \pm$ SD	Range
White blood cells	1985	9.6±2.2	5.7–14.9
	1987	13.2±3.6	9.3–16.9
Mature neutrophils	1985	3.6±1.1	2.4–6.5
	1987	4.5±1.0	3.3–7.8
Lymphocytes	1985	3.1±1.0	0.9–5.8
	1987	4.2±1.4	1.5–6.9

Adrenocortical hormones were analyzed using I^{125} radioimmunoassay kits for cortisol (New England Nuclear, Boston, MA) and aldosterone (Inter-Medico, Willowdale, Ont.). Inter- and intra-assay coefficients of variation for pooled samples of beluga plasma were 13.5% ($n = 15$) and 6.8% ($n = 10$), respectively for cortisol, and 17.1% ($n = 16$) and 9.9% ($n = 5$), respectively for aldosterone.

Results

Free Ranging

Reference values for the free-ranging population were established from up to 42 whales sampled within 1 h after capture (Table 2). Comparison of mean and median values

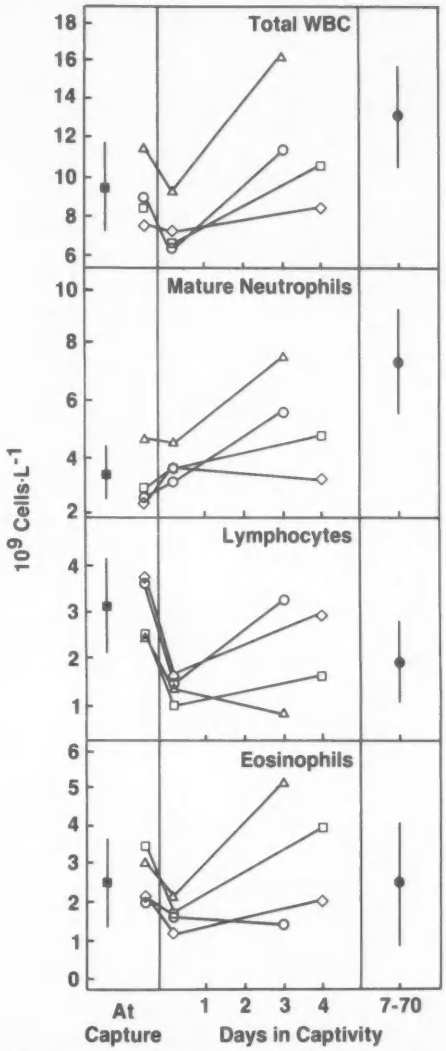

FIG. 1. Changes in leucocyte counts in four beluga whales during the first week in captivity. Mean values and standard deviations (ϕ) are provided for 22 belugas at capture in 1985; acclimated values during the latter 9 wk in captivity are shown as the mean and standard deviation (ϕ) for 25 samples from six whales.

indicated non-Gaussian distributions for aldosterone and alanine aminotransferase. Using a Student *t*-test, no significant difference between males and females was noted in any other blood constituent. Only four or five of the animals were large enough to be sexually mature, and none was physically mature; thus the sample is biased toward subadults. Smaller whales (body length <290 cm; $n = 15$) of both sexes had significantly higher concentrations of alkaline phosphatase ($\bar{x} \pm SD = 269 \pm 110$ versus 165 ± 78 U·L^{-1}; $p < 0.01$, $t = 2.92$) than larger whales (body length 290–381 cm, $n = 14$).

There was wide variation in total and differential leucocyte counts; no correlation was apparent with general condition as assessed by external examination and girth measurement. Total leucocyte counts were significantly ($p < 0.01$) higher in whales

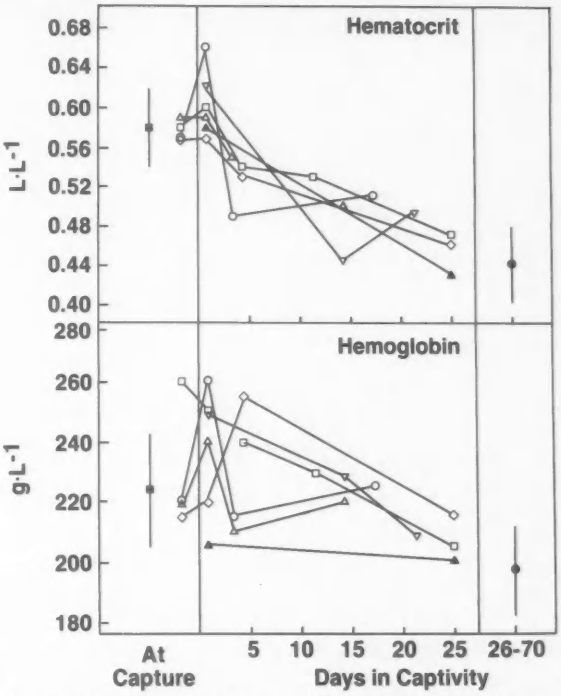

FIG. 2. Progressive decline in hematocrit and hemoglobin concentration in six belugas during the first 25 d in captivity. Mean values and standard deviation (ϕ) are provided for 22 whales at capture in 1985; acclimated values from days 26–70 in captivity are shown as the mean and standard deviation (ϕ) for 18 samples from six whales.

sampled in 1987 than in those from 1985, due primarily to higher lymphocyte and mature neutrophil counts (Table 3). Marked eosinophilia (10.2 cells·L^{-1}) in a whale captured in 1987 was responsible for the highest total leucocyte count (24.3 cells·L^{-1}) observed in either year. Hematologic data from this animal were excluded from the statistical analyses.

Sampling time after capture, which followed a variable chase period, affected only the activity of creatine kinase (CK) in one whale. Samples collected within 30 min after capture ranged between 44 and 376 U·L^{-1}; the one obtained after 55 min had CK activity of 499 U·L^{-1}. If the latter sample is excluded, the recalculated overall mean is 215 ± 78 U·L^{-1}, and the mean value for large whales is reduced to 185 ± 76 U·L^{-1} ($n = 16$), significantly lower than for small whales (245 ± 64 U·L^{-1}, $n = 18$, $t = 2.498$, $p < 0.01$).

Transportation and Acclimation

Four of the six whales taken into captivity in 1985 were sampled immediately after capture, and again on arrival at the holding facilities, 2–3 h later. Total leucocyte counts decreased 20–30% during transportation, then recovered over the next 3–4 d to levels up to 30% higher than at capture (Fig. 1). This elevation, which persisted throughout the remaining 9 wk in captivity, was due to a two-fold increase in mature neutrophils. The early decline in total leucocyte counts reflected changes in lymphocytes and eosinophils, which decreased 30–40% within 2–3 h after capture. During the following weeks, eosinophil counts recovered to levels observed at capture, whereas lym-

TABLE 4. Blood chemical constituents that remained stable in six whales during transportation and throughout 70 d in captivity.

Constituent	Units	N	$\bar{x}$	SD	Range
Sodium	$mmol \cdot L^{-1}$	38	158	6	145–168
Calcium	$mmol \cdot L^{-1}$	39	2.39	0.18	1.86–2.68
Chloride	$mmol \cdot L^{-1}$	38	113	4	105–120
Inorganic phosphorus	$mmol \cdot L^{-1}$	38	2.17	0.38	1.16–2.86
Alkaline phosphatase	$U \cdot L^{-1}$	35	141	67	13–293
Lactic dehydrogenase	$U \cdot L^{-1}$	21	210	145	8–550
Urea	$mmol \cdot L^{-1}$	39	19.0	3.8	10.9–25.7
Uric acid	$\mu mol \cdot L^{-1}$	39	23	21	0–89

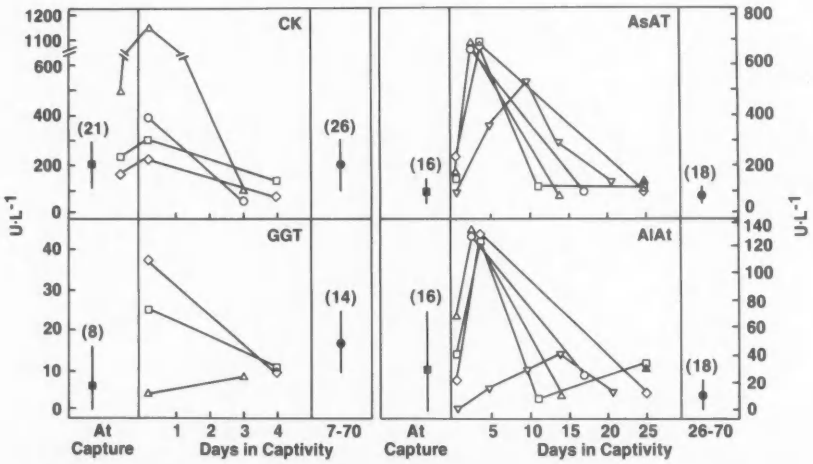

FIG. 3. Transient increases in plasma enzyme activity in beluga whales after capture. Shown in parentheses are the numbers of samples used to calculate the mean and standard deviation at capture (♦) in the 1985 sample group, and after recovery (♦) in the six captive whales.

phocyte counts remained suppressed throughout 10 wk of captivity.

Red blood cell mass, as reflected by packed cell volume, declined progressively during the first 3–4 wk in captivity, reaching a mean value 20–25% lower than at capture (Fig. 2). Parallel changes were noted in Hb; MCHC, calculated as the ratio of PCV and Hb, was therefore relatively stable at an average of 433 ± 36 $g \cdot L^{-1}$, significantly ($p < 0.01$) higher than in free-ranging whales. Since red blood cell counts were not performed on the captive animals, the other red cell indices, MCV and MCH, could not be computed.

Eight plasma chemical constituents showed no trend or significant variation between the time of capture and the last sample taken after 70 d of captivity (Table 4). Others did change, however, as a result of the exertion associated with capture. These included increases in four circulating enzymes (Fig. 3), adrenocortical hormones, and glucose (Fig. 4). Iron and potassium decreased significantly (Fig. 5). After 3–4 d, normal ranges were restored for all but the aminotransferases and iron, which showed a more gradual recovery over the next 2–4 wk.

Cholesterol levels in the captive whales fluctuated widely during the first 6 wk, before stabilizing within a narrow range (Fig. 6). During this time, triglycerides increased steadily and creatinine levels fell (Fig. 6).

Discussion

Blood constituents have long been considered to be sensitive indicators of an animal's health. Pathological conditions can be diagnosed on the basis of subtle changes in cellular elements, metabolites, and enzymes, though proper interpretation relies on understanding the influence of normal physiological activities. This information can be difficult to acquire. In free-ranging animals, the capture effort itself can influence some blood constituents, and captivity others. This study provided a rare opportunity to monitor changes during the critical early stages of acclimation, and thereby distinguish truly representative baseline values from those induced by manipulation and environmental conditions.

We noted two major phases in the acclimation process. During the acute phase, adrenal stimulation and muscular exertion associated with chase and capture affected a number of constituents. In fact, potassium and creatinine were already elevated in the first samples drawn. Many of these changes normalized within the first week, whereas others responded gradually as the animals adapted to the new environment. It is during this second phase that we identify the constituents redefined by captivity.

For most analyses, reference data reported here are similar to those noted in the same population of belugas in 1967 (Geraci et al. 1968a, 1968b), with one major difference. In this study, erythrocytes were larger and more numerous, resulting in 35% higher red cell mass. Since the data were obtained using manual techniques in the earlier study and automated instrumentation in the present work, we compared the results of both methods in samples obtained in 1987 and found no significant differ-

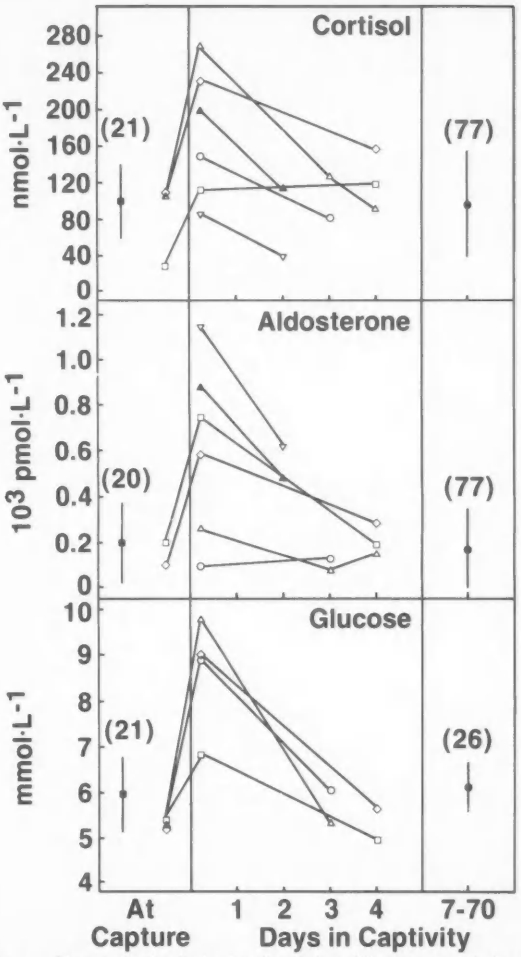

FIG. 4. Changes in circulating levels of adrenal hormones and glucose in beluga whales after capture. Shown in parentheses are the numbers of samples used to calculate the mean and standard deviation at capture (♦) in the 1985 sample group, and after recovery (♦) in the six captive whales.

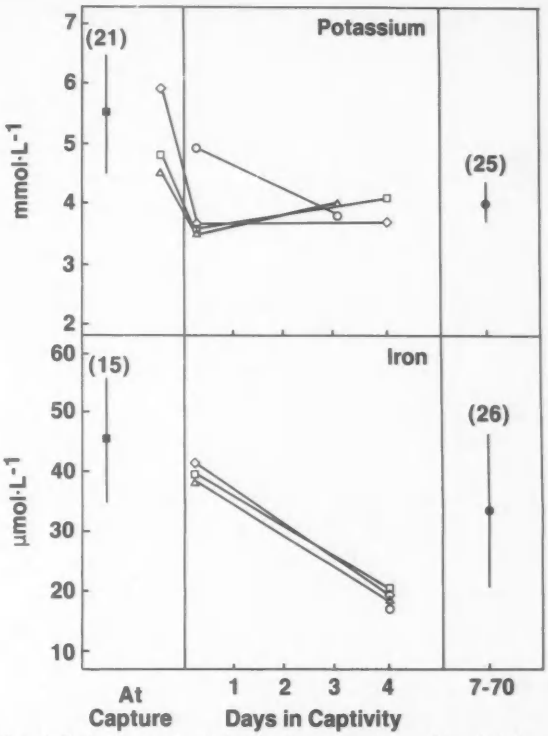

FIG. 5. Reduction in circulating levels of potassium and iron in beluga whales after capture. Shown in parentheses are the numbers of samples used to calculate the mean and standard deviation at capture (♦) in the 1985 sample group, and the acclimated values (♦) in the six captive whales.

ence. A physiological basis for this finding will be addressed later in the discussion.

Chase, capture, and transportation led to elevations of cortisol and aldosterone. The response was similar to that observed in captive bottlenose dolphins, *Tursiops truncatus*, subjected to moderate handling stress (Thomson and Geraci 1986). In both species, aldosterone was the more sensitive indicator of adrenal activity during stress. The prominence of the aldosterone response in cetaceans, as in seals (Johnson-Kocal 1985; St. Aubin and Geraci 1986), draws our attention to the need for marine mammals to secure salt and water balance at such times.

Elevated cortisol levels mediate physiological changes that are reflected in blood. The observed neutrophilia, eosinopenia, and lymphopenia are typical responses following adrenal stimulation or glucocorticoid administration in domestic species (Schalm et al. 1975) and in *Tursiops* (Medway and Geraci 1964; Medway et al. 1970; Thomson and Geraci 1986). Glucose levels increase as a result of cortisol-mediated reduction in peripheral utilization and stimulation of gluconeogenesis (Pugh 1968). Iron shows an opposite trend, possibly to protect against organisms that might take advantage of impaired immune function (Finkelstein et al. 1983). We consider that low plasma iron in recently captured belugas is an adaptive response and not, as implied by Ridgway et al. (1970), an indication that the animals require iron supplements.

There was sufficient muscular activity during capture to release intra-cellular potassium, creatinine, and enzymes. In exercising humans, potassium efflux from muscle cells is mediated by catecholamines (Williams et al. 1985). High values after chase only signal a pathologic state if sustained. Within 3 h, potassium values in the captive belugas declined to a range in line with that of other cetaceans (Ridgway et al. 1970; MacNeill 1975; Cornell 1983; Medway and Geraci 1986). Similarly, creatinine levels in the capture sample were elevated beyond a range traditionally accepted for mammals (Duncan and Prasse 1986). By 7–14 d values declined and stabilized. It is unlikely that early elevations reflected renal dysfunction since urea nitrogen, which is also cleared by the kidneys, was unaffected. Circulating creatinine can be elevated by exercise (Refsum and Stromme 1974), and the rapid initial fall may reflect recovery to normal levels. Thereafter, there was a more subtle decline, associated perhaps with a reduction in the creatine pool which, in turn, is proportional to muscle mass. Creatinine and potassium are thus two constituents which should not be used to evaluate the health of a newly acquired specimen.

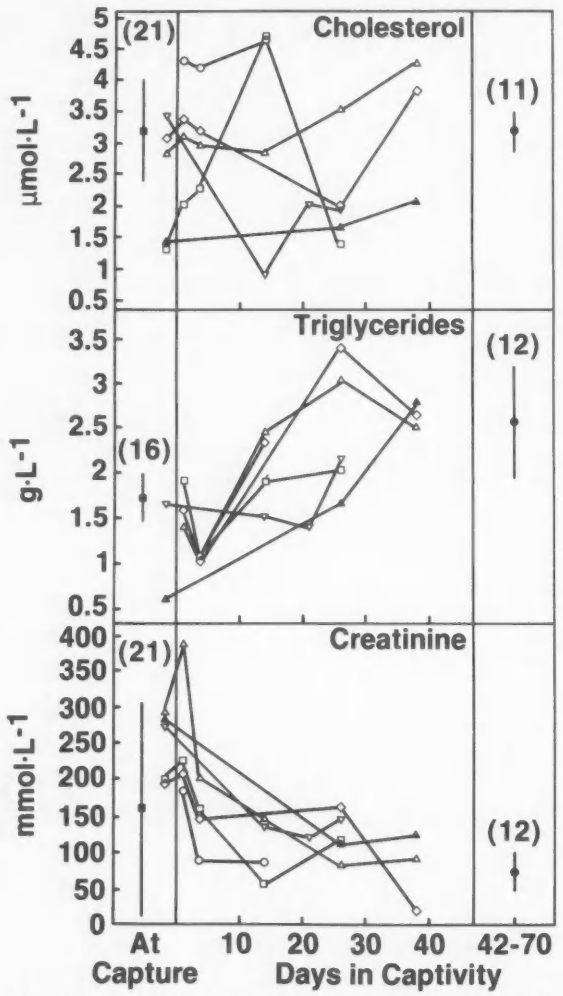

FIG. 6. Changes in plasma cholesterol, triglycerides, and creatinine in six beluga whales during the first 6 wk in captivity. Shown in parentheses are the numbers of samples used to calculate the mean and standard deviation at capture (♦) in the 1985 sample group, and the acclimated values (♦) in the six captive whales.

Circulating enzymes demonstrated that some muscle and liver damage had occurred during or shortly after capture. CK levels rose first; elevated values were evident within 1 h, and in one whale, were well beyond physiological limits by 2–3 h. These changes occur in other species (Sanders and Bloor 1975; St. Aubin et al. 1979; Kock et al. 1987), and are consistent with the high concentration of the enzyme in cetacean muscle (Geraci and St. Aubin 1979). Release from muscle probably also accounts in part for the four-fold increase in AsAT, 2–3 d after capture. The exact contribution by muscle is not clear because the enzyme is also abundant in cetacean liver (Geraci and St. Aubin 1979), and is released with damage to that organ. In the present study, parallel changes in AlAT, another liver-specific enzyme, indicate some leakage from hepatic stores. It may have been secondary to inadequate perfusion and anoxia as a result of stress-induced circulatory insufficiency (Fojt et al. 1976). Further evidence of liver damage can be drawn from the elevated levels of γ-GT in two of three whales, though these changes are more suggestive of biliary stasis than hepatocellular necrosis (Meyer 1983). The problem resolved by the third week in captivity, as indicated by the return of circulating enzymes to stable baseline values.

Certain metabolites and formed elements provided evidence of metabolic adjustments to captivity, unrelated to the stress and manipulation associated with capture. Plasma levels of triglycerides first dipped then rose progressively to relatively stable values somewhat higher than those at capture. Cholesterol values fluctuated widely, also to stabilize by the sixth week. This pattern suggests a change in the whales' lipid metabolism, perhaps influenced by the nature and quantity of their food intake. During the first few weeks, the whales ate sparingly and all lost weight. Their natural diet at this time, principally decapod crustaceans (Sergeant 1973), was replaced with lipid-rich Pacific herring, which four of the whales consumed at levels insufficient to maintain body weight. It would be interesting to examine these plasma indicators of lipid homeostasis during natural cycles of feeding and fasting.

Geraci et al. (1968b) noted differences in leucocyte counts between free-ranging and captive belugas. Similar findings, notably an increase in neutrophils and a reduction in lymphocytes and eosinophils, were observed in our belugas acclimated to captivity. Neutrophilia was probably a response to continued challenge from infectious organisms. The decline in eosinophils and lymphocytes suggests that glucocorticoids were released periodically as the whales were handled for other studies. Reduced eosinophil counts are probably of little functional consequence, though similar changes in lymphocytes might conceivably affect an animal's immune capacity. These findings underscore the need for more penetrating studies into humoral and cell-mediated immunity in cetaceans.

Hematocrit declined steadily in the belugas during the first 3 wk in captivity. In cetaceans, red cell mass correlates with oxygen demand and activity; values are higher in fast-swimming, deep diving species (Ridgway and Johnson 1966) and individuals (Ridgway et al. 1970, 1984; Duffield et al. 1983). Hence the changes in captivity probably reflect a reduced need for oxygen carrying capacity in blood, and represent an economy of cardiopulmonary effort. This adaptation may explain the marked difference in hematocrit values between the whales in this study and those from the same population sampled nearly 20 yr earlier (Geraci et al. 1968b). The animals sampled on August 1–4, 1967 had hematocrit values of $0.42 \pm 0.02\ L \cdot L^{-1}$, compared with the present values of $0.59 \pm 0.04\ L \cdot L^{-1}$ in whales sampled on July 2–4, 1985 and July 18–20, 1987; there was no significant difference between the 1985 and 1987 study groups. Sampling date is an obvious variable in the study, and for belugas, time of year relates to habitat. In early July, animals begin to move from deep offshore waters to shallow estuaries where they remain until early September (Sergeant 1973). Thus, the animals sampled in 1985 were recent arrivals, among the first observed that year, whereas those examined in 1967 had likely been in shallow water for several weeks. Our data show that the decline in hematocrit can occur within this time frame. Perhaps the relatively high red cell mass in the whales sampled in the latter part of July 1987, indicates that many of these animals had spent a comparatively short time in shallow water. The suggestion calls for a study on identifiable whales with known arrival dates or patterns of occupation in the estuaries. If the assumption is correct, it is the first evidence that dynamic

hematologic changes accompany normal cyclical events in a cetacean. For those keeping or studying whales, it is useful to recognize that such changes in hematocrit do not necessarily signal a pathologic state.

This study demonstrates how blood values can be influenced by the very nature of the study required to obtain the results. Capture triggers the adrenal stress response with attendant elevations in aldosterone and cortisol, and consequent changes in glucose, iron, lymphocytes and eosinophils. The activity associated with the chase releases intramuscular potassium, creatinine, CK, and AsAt into circulation. Once in captivity, recovery of these constituents is rapid, but then other changes appear. A delayed and yet unexplained effect on the liver was evident from an increase in enzymes normally associated with hepatocellular damage. The problem, which resolved within 3 wk, may have been compounded by the abrupt change in diet and feeding behavior imposed on the animals. Triglycerides and cholesterol, which are indeed related to diet, certainly were affected. While all of these constituents eventually stabilized at what we would consider to be normal values, it was apparent that others would attain a new equilibrium in tune with the captive environment. This was particularly evident by the way in which red blood cell mass declined and neutrophils rose in the acclimating animals; adjustments in circulating levels of thyroid hormones have already been reported (St. Aubin and Geraci 1988). The sustained decline in lymphocytes may be important with respect to the immunologic status of such animals. This and the role of iron in disease would offer potential for studies into ways to improve the health and longevity of these animals in captivity.

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Ontogenetic Variation in the Multiple Hemoglobins of Arctic Charr, *Salvelinus alpinus*

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Giles, M. A., and D. M. Rystephanuk. 1989. Ontogenic variation in the multiple hemoglobins of Arctic charr, *Salvelinus alpinus*. Can. J. Fish. Aquat. Sci. 46: 804–809.

Changes during development in the multiple hemoglobins of hatchery-reared Arctic charr, *Salvelinus alpinus*, that originated from an anadromous stock from Nauyuk Lake, Northwest Territories were examined by starch gel electrophoresis. A total of 10 anodic and 7 cathodic hemoglobins were expressed during the life cycle of the charr. Embryos and newly-hatched alevins exhibited 10 anodic and 3 cathodic components. Of these embryonic hemoglobins, 5 anodic components and possibly 1 cathodic component with similar electrophoretic mobility were observed in older fish. In free-swimming fry 3–4 new cathodic components were expressed. Two phenotypes (designated as 3-C or 5-C) were identified in postembryonic charr, distinguished by the presence of either 3 or 5 cathodic hemoglobins, respectively. In both phenotypes the proportion of cathodic hemoglobins increased progressively with age to a maximum of 22 and 18% of total hemoglobin in the 3-C and 5-C phenotypes, respectively.

Par électrophonèse sur gel d'amidon, on a étudié les changements qui se produisent durant le développement dans les hémoglobines de l'omble chevalier (*Salvelinus alpinus*) d'élevage issu d'un stock anadrome du lac Nauyuk dans les Territoires du Nord-Ouest. On a constaté qu'en tout il se forme 10 hémoglobines anodiques et 7 cathodiques durant le cycle biologique de l'omble. On a trouvé 10 composants anodiques et 3 cathodiques chez les embryons et les alevins fraîchement éclos. Chez les poissons plus avancés, il y a 5 composants embryonnaires anodiques, et peut-être un composant cathodique, de mobilité électrophorétique semblable. Chez les alevins libres, il y a 3 ou 4 autres composants cathodiques. L'omble post-embryonnaire peut avoir l'un ou l'autre de deux phénotypes : le phénotype 3-C, à 3 hémoglobines cathodiques et le phénotype 5-C, à 5 hémoglobines cathodiques. Dans les deux cas, la proportion d'hémoglobine cathodique augmente progressivement à mesure que le poisson vieillit, pour représenter 22 % du total d'hémoglobine chez le 3-C et 18 % chez le 5-C.

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Hemoglobin polymorphism is more extensive in fishes than in any other vertebrate group, both in terms of the proportion of species exhibiting multiple hemoglobins and in the degree of heterogeneity in individual species. Among fishes, salmonids generally exhibit the highest degree of hemoglobin polymorphism with some species expressing up to 18 distinct components (Wilkins 1968; Tsuyuki and Ronald 1971; Giles and Vanstone 1976).

Ontogenetic changes in the number of hemoglobins have been reported for more than a dozen species of fish. While most of these studies have examined fish at two distinct ages, a few have reported the detailed changes in hemoglobin composition and/or concentration over the life cycle. Among salmonids qualitative and quantitative changes in the polymorphic hemoglobins with age have been described for Atlantic salmon, *Salmo salar* (Wilkins 1968; Westman 1970; Koch 1982), rainbow trout, *Salmo gairdneri irideus* (Iuchi and Yamagami 1969), and coho salmon, *Oncorhynchus kisutch* (Giles and Vanstone 1976). In these species a general trend exists in that all exhibit an increase with age in the proportion of hemoglobins with more acidic isoelectric points (cathodic hemoglobins). In coho salmon (Giles and Vanstone 1976; Sullivan et al. 1985) and pink salmon, *O. gorbuscha* (M. A. Giles, unpubl. data), a major increase in the cathodic hemoglobins occurs during the smoltification process and may have some physiological significance in terms of blood–gas transport during the extensive marine migrations undertaken by these fish (Giles and Randall 1980). In Atlantic salmon, however, no changes in hemoglobin pattern could be associated with smoltification (Wilkins 1968). Furthermore, both rainbow trout and coho salmon express a distinct set of embryonic hemoglobins which disappear upon attaining the free-swimming stage (Iuchi and Yamagami 1969: Giles and Vanstone 1976).

When compared with Pacific salmon, the life cycle of anadromous Arctic charr is highly plastic in terms of length of juvenile freshwater residence, age at smolting, period of freshwater residence of sexually mature spawners and number of reproductive cycles experienced. In this respect the charr may resemble more closely the Atlantic salmon. Features which indicate the onset of smoltification, such as loss of parr marks, are not well defined for natural populations of charr (Johnson 1980), and may have significant consequences for mariculture of this fish. This study was undertaken to identify the hemoglobin polymorphs expressed during the life cycle of a stock of hatchery-reared Arctic charr derived from an anadromous population. A secondary purpose was to determine if any episodes of hemoglobin development existed which could be indicative of major changes in physiological status such as smoltification.

Methods

Arctic charr were obtained from stocks reared at the Rockwood Experimental Fish Hatchery, Gunton, Manitoba. The anadromous Nauyuk Lake stock, used in this study, originated

from the spawn of two male and two female adults collected upon their return from the Arctic Ocean to Nauyuk Lake, Northwest Territories (68°21′N; 107°40′W) in November 1978. The electrophoretic identity of the hemoglobin of these four charr was not determined. The fertilized eggs were disinfected with a 1% solution of "Bridine" (BDH Pharmaceuticals Ltd.) at the spawning site, transported by air to the Freshwater Institute, Winnipeg, Man., and incubated to the "eyed" stage in a Heath incubator at 5.4°C. The eyed eggs were moved to the Rockwood Hatchery and reared at 6.5°C. Adults raised from these eggs formed the hatchery parental stock. These fish were the parents of all subadult fish (age <100 wk) employed in this study. The hemoglobin electropherograms of charr at ages of 24, 47, and 99 wk were obtained from the 1982, 1983, and 1984 matings of these hatchery-reared adults while the adults themselves were used as the oldest age group (>300 wk). The spawners, developing eggs, and alevins were maintained at 6.5°C whereas juveniles were reared at 10–12°C. Details of the rearing conditions are described by Baker (1983) and Tabachek (1984). All ages in this study designate the date of fertilization as day 0. At 6.5°C hatching began 44 d after fertilization and was complete within 16 d. A number of adults in the parental stock were individually marked with coded tags and used in selected matings to investigate the genetic basis for the multiple hemoglobins of charr. These fish and the resultant eggs were treated in the same manner as described previously.

Blood was collected from small fish in heparinized capillary tubes from the severed caudal peduncle. Larger fish were anesthetized in buffered tricaine methanesulfonate (1:5000, Sigma Chemical Co.) and blood collected by syringe from the dorsal aorta in the roof of the mouth. Samples were obtained from newly-hatched alevins or unhatched embryos immediately prior to hatch by placing the egg or alevin into heparinized 0.9% NaCl in a glass dish, then severing the caudal peduncle and collecting the blood in capillary tubes. The erythrocytes were separated by centrifugation, washed thrice with Cortland saline (Wolf 1963) and the hemoglobin converted to the carboxy-form with carbon monoxide. The cells were suspended in 1–2 volumes of distilled water and frozen. The samples were thawed and the hemolyzate separated from the cell debris by centrifugation. All preparations were performed at 0–4°C and all samples subjected to electrophoresis within 24 h of blood collection.

Electrophoretic separation of the hemoglobins was conducted using the micro-starch gel method of Tsuyuki et al. (1966) at pH 8.6 and a constant voltage of 200 V for 90 min at 0°C. The current did not exceed 2.3 mA per strip. Gels were stained in 0.1% Amido Schwartz B in acetic acid:methanol:water (1:5:5, by volume) for 15 min and destained for 1–2 d in the same solution without stain. The gels were photographed using transmitted light and the negatives scanned at 660 mμ in a Gilford spectrophotometer (model 2400) equipped with a linear transport carriage, a 0.05 × 2.36 mm slit plate, and a Gilford variable span recorder. Approximately 70 gels were also cleared by careful heating in a solution of glycerin:methanol:water (2:1:7; by volume) and scanned at 600 mμ. The area under each peak and its mobility from the origin was determined from the recorder tracing with a Hewlett-Packard digitizer (model 9864A). The relative mobilities of the components were expressed as a ratio to the distance travelled by an easily identified major component (Hb band A6) which was present in all life stages. The relative concentration of each component was expressed as a percentage of the total complement of hemoglobins. The relative concentrations of the components of embryonic and alevin hemoglobins were not determined since the electropherograms were relatively faint. The relative mobilities of these components were derived from micrometre measurements of each band directly on the gels.

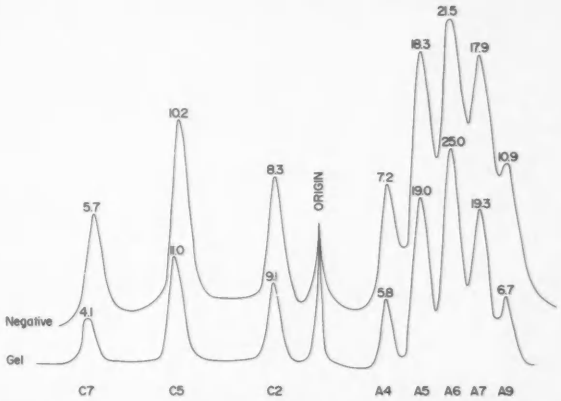

FIG. 1. Comparison of spectrophotometric scans of hemoglobin components in cleared starch gels and in the photographic negatives of the same gel. The numbers under the peaks are estimates of the relative concentration of each component derived from their respective scans.

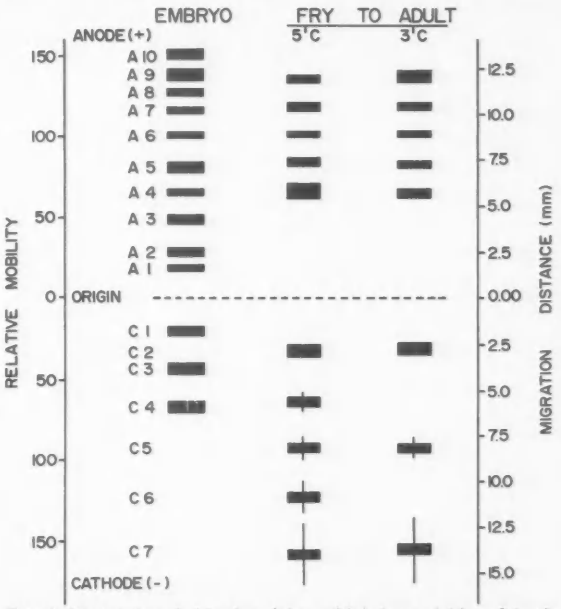

FIG. 2. Electrophoretic identity of the multiple hemoglobins of Arctic charr. The vertical bars represent the variation in relative mobility as a proportion of the mobility of component A6. The actual migration distance (± 1 SD) of component A6 in a sample of 47 electropherograms from embryos, juveniles, and adults was 8.8 (± 1.09) mm.

Although the results are presented as percentages for purposes of clarity all statistical treatment of proportional data were performed after angular transformation (Steel and Torrie 1960).

Results

Estimates of Hemoglobin Relative Concentration

A regression of the relative concentration of hemoglobin components derived from spectrophotometric scans of

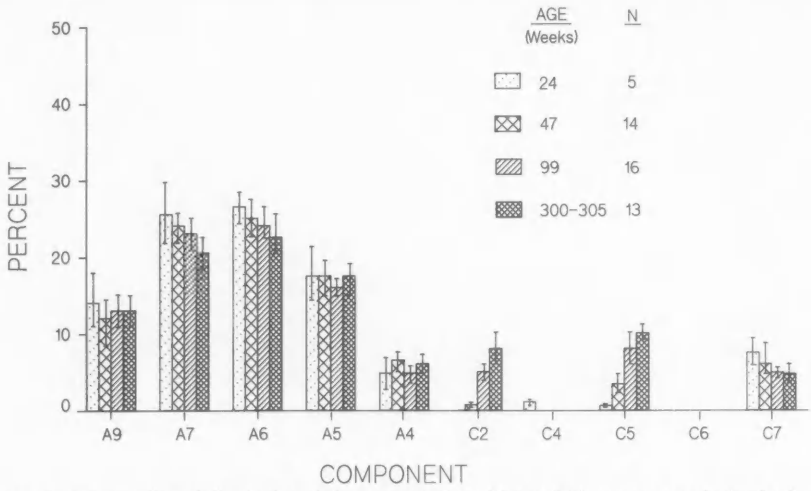

FIG. 3. Ontogenetic variation in the relative concentration of hemoglobin components in Arctic charr exhibiting the 3-C phenotype. Vertical lines indicate ± 1 SD of the mean calculated from the angular transformation of the original percentages and *N* indicates the number of fish in each age group.

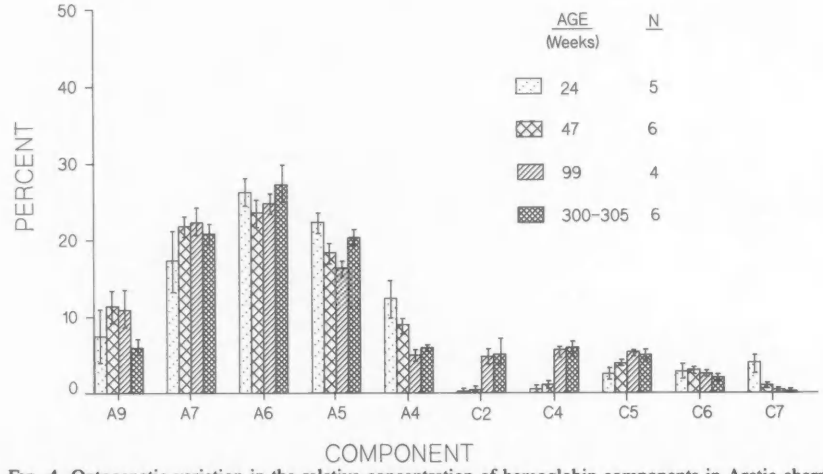

FIG. 4. Ontogenetic variation in the relative concentration of hemoglobin components in Arctic charr exhibiting the 5-C phenotype. Legend details as in Fig. 3.

photographic negatives versus their corresponding gels did not yield a 1:1 relationship. The regressions for 625 pairs of electrophoretic bands were;

$$N = 0.977 + 0.902G \qquad R^2 = 0.942$$
$$N_t = 0.737 + 0.942G_t \qquad R^2 = 0.942,$$

where N and G denote paired relative (percent) concentrations from negatives and gels, respectively, and the subscript t denotes the angular transformation of the percent values. The standard errors of estimate for N and the coefficient of G were 1.9813 and 0.0090, respectively, for the percentage data and 1.9868 and 0.0095, respectively, for the transformed data. These relationships indicate that the negatives tend to underestimate very low relative concentrations and overestimate high relative concentrations, but do provide a reasonable estimate for the majority of hemoglobin components examined in this study. The scans of the negatives also reduced the separation of the components (Fig. 1) which may have had the effect of artificially increasing the proportions of A4 and A9 because of spill-over from the dense adjacent components. Since the gels are fragile and difficult to clear in a uniform manner the estimates of the fractional composition of the hemoglobin polymorphs presented in the following sections were derived from scans of the photographic negatives. All percentage data were subjected to the angular transformation prior to statistical analysis since proportions do not exhibit a normal distribution. The individual hemoglobins are identified by a letter/number code with the letter designating the direction of migration (anodic and cathodic) and the number designating the rank of the distance the component moved in that direction.

Ontogenetic Variation

A total of 17 hemoglobins were expressed during the life span of Nauyuk Lake Arctic charr and of these only five (A4,

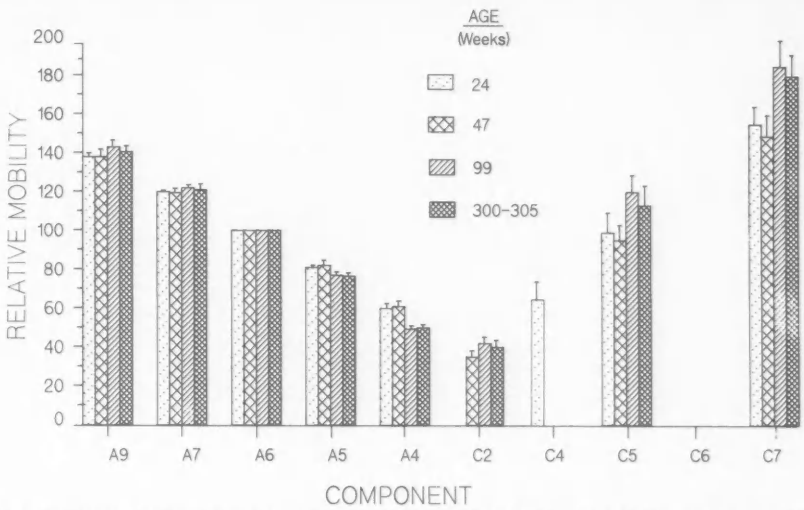

FIG. 5. Changes in the relative electrophoretic mobility with age of the hemoglobin components of 3-C phenotype Arctic charr. The vertical lines indicate 1 SD of the mean.

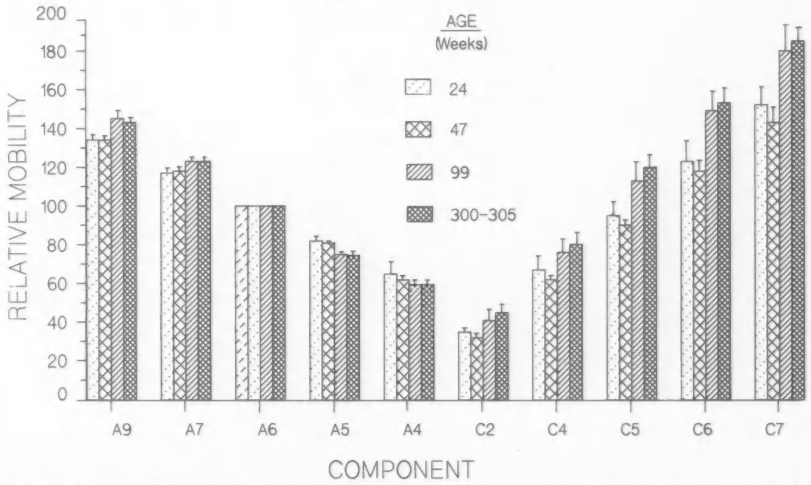

FIG. 6. Changes in the relative electrophoretic mobility with age of hemoglobin components of 5-C phenotype Arctic charr. Legend details as in Fig. 5.

A5, A6, A7, and A9) were present in all life stages (Fig. 2). Blood from unhatched embryos and newly hatched alveins (44–60 d after fertilization) had 10 anodic and three cathodic components of which five anodic (A1, A2, A3, A8, and A10) and two cathodic (C1 and C3) had disappeared by the time the fish had grown to approximately 0.35 g (170 d postfertilization). Two phenotypic hemoglobin patterns were observed in the fry to adult life stages. Although the patterns differed in their complement of cathodic hemoglobins both exhibited five electrophoretically identical anodic components (A4, A5, A6, A7, and A9) retained from the embryonic stage. In one group, designated as the 3-C phenotype (Fig. 2), hemoglobin C5 and C7 appeared by 24 wk and C4 was retained from the embryonic pattern. During the interval of 24–47 wk hemoglobin C4 was eliminated and C2 appeared in the 3-C phenotype (Fig. 3). In the second phenotype, designated as 5-C, hemoglobin C4 was retained from the embryonic stage and C2, C5, C6, and C7 appeared by 24 wk of age. No further changes in the number of components were observed during development in either phenotype although substantial changes in the relative concentrations of the individual hemoglobins did occur.

The individual hemoglobins of the 3-C phenotype exhibited consistent changes with age (Fig. 3). Components C2 and C5 increased while C7 decreased with age. Overall, the cathodic hemoglobins increased to 9.0, 10.5, 17.5, and 21.9% of total hemoglobin at 24, 47, 99, and >300 wk of age, respectively. These increases corresponded to decreases in A6 and A7 since A4, A5, and A9 remained unchanged in all age groups.

Charr of the 5-C phenotype exhibited a biphasic increase in the proportion of cathodic components (Fig. 4). At 24 and 47 wk cathodic components accounted for 9% of the total hemoglobin versus 18% at 99 and >300 wk. In general C2, C4, and

TABLE 1. Summary of the inheritance of 3C and 5C hemoglobin phenotypes. NI = phenotype not identified. *; Chi-square = 0.81, p = 0.4, not significant.

Parents	Number of Progeny	
F × M	3-C	5-C
3-C × 5-C	14	12
3-C × 5-C	10	14
5-C × 3-C	12	14
NI × 5-C	17	8
3-C × 5-C	14	9
Total 3-C × 5-C	67	57*
3-C × 3-C	6	0
3-C × 3-C	16	0
3-C × 3-C	6	0
3-C × 3-C	6	0
3-C × 3-C	6	0
Total 3-C × 3-C	40	0

C5 increased between the two stages, while C7 declined and C6 remained constant. No clear pattern was evident in the pattern of change for most individual anodic components, although the concentration of A4 declined by 50% from 24 to >300 wk.

Changes with age were observed in the relative mobility of individual hemoglobin components in both 3-C and 5-C phenotypes (Fig. 5 and 6). A general trend to increased mobility of all cathodic components with increasing age was evident while the slower moving anodic components (A4, A5) tended to migrate less with increasing age. No differences were observed between phenotypes in the mobilities of the components common to both the 3-C and 5-C phenotypes for fish at any particular age.

Inheritance of 3-C and 5-C Phenotypes

Of twenty-four pairs of adult, hatchery-reared charr which had been individually mated only 10 pairs produced viable offspring. The F-1 (Table 1) of 3-C × 3-C matings were all 3-C phenotypes, whereas 3-C × 5-C matings produced approximately equal numbers of 3-C and 5-C offspring. Unfortunately no successful 5-C × 5-C matings were obtained. The sex of the parent exhibiting the 5-C phenotype had no effect on the ratio of the 3-C:5-C phenotypes in the offspring. These observations suggest that the 3-C parents were homozygous at the locus coding for the most positively charged hemoglobin subunit. The 5-C phenotype evidently represents a heterozygous genotype.

Discussion

Nauyuk Lake charr exhibited either 16 or 17 electrophoretically distinct hemoglobins during their life span. Two phenotypes were observed; the 3-C phenotypes in which 16 hemoglobins were expressed and the 5-C phenotype in which 17 hemoglobins were expressed. Only 5 anodic components were present in all fish at all developmental stages. Two phases were evident in hemoglobin expression; an embryonic phase (10 anodic and 3 cathodic components) and a postembryonic phase in which 5 anodic components are retained and 3–4 new cathodic components are expressed while the remaining hemoglobins disappear. Although quantitative changes in the proportions of the postembryonic hemoglobins occurred during the next several years the phenotypic pattern remained constant. During this time the cathodic components increased by twofold to 18 and 22% of the total hemoglobin for the 5-C and 3-C phenotypes, respectively.

Ontogenetic changes in polymorphic hemoglobins have been reported in a diversity of fishes, including lamprey, *Petromyzon planerii* (Adinolfi et al. 1959), dogfish shark, *Squalus suckleyi* (Manwell 1963), European eel, *Anguilla anguilla* (Rizzotti et al. 1977), herring, *Clupea harengus* (Wilkins and Iles 1966), and a variety of trout and salmon (Vanstone et al. 1964; Wilkins 1968; Iuchi and Yamagami 1969; Tsuyuki and Ronald 1971; Giles and Vanstone 1976). Few of these studies have included embryonic life stages. Embryonic and newly-hatched Arctic charr appear to exhibit a similar multiplicity of cathodic hemoglobins as observed in rainbow trout (Iuchi and Yamagami 1969), coho salmon (Giles and Vanstone 1976), and pink salmon (M.A. Giles, unpubl. data). The reduction in the number of anodic components and the increase in the number and relative concentration hemoglobins with more acidic isoelectric points (cathodic components) with increasing age was similar in Arctic charr to that described for other salmonids. Koch (1982) observed a 10% decrease in the relative concentration of the anodic hemoglobins of Atlantic salmon as the fish increased in size from 15 to 45 g. This same decrease in anodic hemoglobin concentration occurred in the present study in charr older than 47 wk when the fish were about 10–15 g in weight. The total proportion of anodic hemoglobins was consistently higher in Arctic charr (78–90%) than the 52–62% reported by Koch (1982) in the Atlantic salmon. In both of these salmonids, however, the changes in hemoglobin concentration were gradual with increasing age.

The abrupt increase in concentration of cathodic components associated with parr–smolt transformation in coho salmon in freshwater (Giles and Vanstone 1976; Sullivan et al. 1985) was not observed in the charr. Although this Nauyuk Lake stock of charr originated from anadromous parents, the age at which juveniles undergo smoltification and seaward migration is quite variable (Johnson 1980). The charr in the present study were not exposed to the cycles in temperature, photoperiod, and ice cover that occur in their home environment. It is possible, therefore, that had such cues been present some differences in the pattern of hemoglobin would have occurred. It should be noted, however, that exposure to various levels of temperature, dissolved oxygen, and salinity did not influence age related changes in the hemoglobins of presmolt coho salmon (Giles and Vanstone 1976).

The subunit structure of individual hemoglobin polymorphs has been identified in several salmonids (Wilkins 1970; Ronald and Tsuyuki 1971; Tsuyuki and Ronald 1971). Each is a tetramer, composed of two, three, or four different subunits, from the complement of seven to eight subunits identified in each species. Although not determined in the present study, it is assumed that the hemoglobins of Arctic charr are also tetrameric in structure. The presence of two hemoglobin phenotypes in adult Nauyuk Lake charr can be explained most simply by the occurrence of two alleles at the locus coding for the hemoglobin subunits with the most acidic isoelectric point. The 5-C phenotype thus represents a heterozygous genotype with one allele coding for a subunit having a slightly higher isoelectric point than that produced by the 3-C allele. If both alleles are expressed equally in the 5-C phenotype then the sum of C4, C5, C6, C7 should equal the sum of C5 and C7 in the 3-C phenotype. The sum of the cathodic hemoglobins, excluding

C2, for the 5-C versus the 3-C phenotypes, respectively, was 8.8 versus 8.0%, 8.7 versus 9.9%, 13.6 versus 12.2%, and 12.6 versus 13.8%, for fish at 24, 47, 99, and >300 wk of age, respectively.

It is reasonable to expect that the rearing conditions in the hatchery may affect the rates of growth and development of the charr and thereby change the timing of the expression of the various hemoglobins. Although rate of growth and a variety of environmental cues had no direct effect on the expression of polymorphic hemoglobins in coho salmon (Giles and Vanstone 1976) other evidence suggests that changes in hemoglobin composition may be related to fish size, thyroid activity, stress, growth hormone, and food composition (Koch 1982; Sullivan et al. 1985). Thus the results presented in this study must be regarded as an expression of the potential for ontogenetic changes in hemoglobin composition rather than an exact description of the time course of change.

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Golden Shiner (*Notemigonus crysoleucas*) Population Abundance: Correlations with Food and Predators

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A winterkill at Lake St. George, Ontario eliminated most of the piscivorous fish and some of the planktivores and also influenced zooplankton community structure. This disturbance and the subsequent recovery of the populations provided the opportunity to evaluate potential impacts of food and predators on the population structure and abundance of the dominant planktivore; the golden shiner (*Notemigonus crysoleucas*). Interpretation of the 8-yr data set suggested that there was a positive relationship between adult golden shiner condition and zooplankton abundance, but that this did not translate into a significant stock–recruitment relationship between female numbers and young-of-the-year (YOY) recruitment. Also, there was no significant relationship between golden shiner survival and zooplankton abundance. However, there were significant negative correlations between YOY and adult golden shiner survival estimates and predator abundances. We conclude that at Lake St. George, golden shiner recruitment and population density is strongly influenced by predator density and is not influenced by food abundance.

Une martégade au lac Saint-George en Ontario a éliminé la plupart des poissons piscivores et certains planctophages, et a également influencé la structure des populations de zooplancton. Les troubles qu'ont connu les populations et leur rétablissement subséquent a donné l'occasion d'évaluer les répercussions possibles de la nourriture et des prédateurs sur la structure des populations et l'abondance du planctophage dominant, la chatte de l'est (*Notemigonus crysoleucas*). L'interprétation des données recueillies au cours d'une période de 8 an donne à penser qu'il y a une relation positive entre la condition de la chatte de l'est adulte et l'abondance du zooplancton, mais que cela ne se traduit pas par une relation significative effectif–recrutement entre le nombre de femelles et le recrutement des jeunes de l'année. En outre, il n'y a pas de relation significative entre la survie de la chatte de l'est et l'abondance de zooplancton. Il y a toutefois une corrélation négative significative entre le nombre estimatif de jeunes de l'année et de chattes de l'est adultes et l'abondance des prédateurs.

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Identifying and quantifying the relative importance of factors that regulate populations of freshwater fish are major goals of fisheries biologists and the emerging consensus is that a number of factors play key roles. Impacts of changing food availability on abundance have been studied by numerous authors, e.g. Le Cren (1965); Persson (1983, 1986); Gutreuter and Anderson (1985); and Mills et al. (1987b) and they have shown that available food can limit the flow of energy to a fish population and can thereby limit future abundance through influences on fecundity and growth. The role of predators in determining abundance has been investigated by many authors, e.g. Bonar (1977); Forney (1977); Holčík (1977); Crowder (1980); van Densen (1985); Hurley (1986); and Minns and Hurley (1986) and most agree that predation is often a principal cause of mortality in fish populations, particularly in early life stages. The influence of other factors, particularly temperature and low winter oxygen have been considered by Colby (1973); Casselman and Harvey (1975); Koonce et al. (1977); Shuter et al. (1980); Klinga et al. (1982); Tonn and Magnuson (1982); Rahel (1984); and Henderson and Brown (1985). The consensus is that these factors can be important as periodic disturbances that affect survival of young-of-the-year (YOY) either within a few weeks after spawning or during the first winter.

Our study concentrates on potential impacts of two of these factors, food availability and predation. At Lake St. George, a winterkill eliminated most piscivores and some planktivores and as the populations recovered we gathered data that allowed us to investigate correlative relationships between variability in the abundance of golden shiners (*Notemigonus crysoleucas*) and variability in food and predator abundance.

Study Area

Lake St. George (43°57′30″N, 70°25′30″W) is located in south-central Ontario, and has a surface area of 10.3 ha. It is a dimictic, eutrophic kettle lake with a maximum depth of 15 m and a clinograde oxygen profile (McQueen and Lean 1987). In the summer, fish populations are restricted to the epilimnion.

Study Species

In Lake St. George, as in other lakes, golden shiners feed almost exclusively on limnetic zooplankton; primarily daph-

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nids, but also bosminids and copepods (Cooper 1936; Keast and Webb 1966; Suffern 1973; Hall et al. 1979; Johannes 1987). They are in turn, eaten by largemouth bass, northern pike and large perch (Regier 1963; Keast 1985). Golden shiners spawn during May and June (Cooper 1935; Forney 1957; De Vlaming 1975) and by the end of the first summer, juvenile fish are large enough to recruit into pelagic schools of adult fish.

Materials and Methods

Golden Shiner Abundance

The abundances of golden shiners were estimated in the fall of each year. Estimates in 1984, through 1987 were derived using multiple census mark–recapture experiments (Ricker 1975). Fish were marked with fin clips and recaptured during the next 2 wk. During that time, we attempted to mark >5% of the estimated population. Details are given in McQueen et al. (1989).

Abundances in 1980 through 1983 were estimated by comparing gear catch per unit effort (CPUE) data from these years with similar data from years in which we made mark–recapture estimates of abundance. In the fall of 1980 and 1981, estimates were obtained in two ways: (1) the comparison of beach seine CPUE from 1980 and 1981, with beach seine CPUE from 1984, 1985, and 1986, where estimates were calculated by multiplying the proportion of these CPUEs with mark–recapture abundance estimates (1984, 1985, 1986, and 1987); and (2) from correlated populations, where estimates were derived from the comparison of gear (beach seines and Windermere traps) CPUE for golden shiners to CPUE (similar gear) of species which had been estimated with mark–recapture techniques (Youngs and Robson 1978). Estimates of fall abundance in 1982 and 1983 were derived in two ways: (1) comparison of Windermere trap CPUE from 1982 and 1983, with Windermere trap CPUE in 1984, and (2) comparison of beach seine CPUE from 1982 and 1983 with beach seine CPUE from 1984, 1985, and 1986. The 1982 and 1983 estimates were calculated by multiplying the proportion of these CPUEs (both Windermere traps and beach seines) by mark–recapture abundance estimates (1984, 1985, 1986). Estimates of abundance for 1980 to 1983 were based on the combination of at least two mean estimates (from the previous methods) weighted by CPUE sample sizes to produce an overall mean. The accuracy of the final population estimates was checked by comparing these estimates with other estimates derived from the extrapolation of CPUEs (inshore and offshore) to volumetric density estimates.

Tests for mark induced mortality were conducted during 1984–87. Fin clipped fish were held in 300-L holding tanks for 36 h and the observed mortality rates during these years were 2, 1, 0, and 0%. Abundance calculations were corrected for this capture induced mortality. Tests of gear size selectivity and efficiency were conducted during 1984. All three gear types: (1) 31 m × 1.8 m, 5-mm mesh beach seine, (2) 31 m × 9.8 m, 1-mm mesh purse seine, and (3) 90 cm × 57 cm, 8-mm mesh Windermere traps were fished simultaneously and data showed that the size of fish caught was independent of gear type and location (inshore and offshore) (Chi-square = 2.4, $df = 6$). Catchability was calculated among gears between years by equating a species mark–recapture abundance estimate (spring and fall 1984, 1985, 1986, and 1987) with CPUE data, for both inshore and offshore gear collected simultaneously (Ricker 1975). Catchability estimates for an individual gear were found to be equivalent (regressions of catchability with respect to numbers all had $p < 0.05$) between years suggesting that fish vulnerability for a gear, was independent of abundance. These tests suggested that gear CPUE was proportional to fish abundance and could be used to produce relative abundance estimates among years.

Golden Shiner Length–Weight Relationships

Measurements were taken across a series of fixed length and weight intervals for all ages and both sexes of golden shiners in the spring and fall of each year. Logarithmic length–weight relationships (Ricker 1973, 1975, 1984; Jensen 1986) were tested for slopes significantly different from zero (16 spring and fall (1980–87) length–weight regressions had slopes significantly different from zero, $p < 0.05$) and regression lines among years were compared using analysis of covariance tests for slope and elevation (ANCOVA, $F = 15.57$, $df = 15, 1820$) (Zar 1984). As a measure of the nutritional state of the fish (Bagenal and Tesch 1978) a condition factor (intercept of the geometric mean length versus weight regression) was derived for each year.

Golden Shiner Age at Length

Scales were used to assess golden shiner age (Cooper 1936; Regier 1963; and Forney 1957). Golden shiner age distributions for 1980–87 were estimated by constructing an age–length key from a random sample of length-classes of fish collected from the fall population of each year. These estimates were used to convert length distributions to age (Ketchen 1950). Age–length distributions were converted to age–weight distributions using calculated arithmetic mean length to weight regressions.

Golden Shiner Fecundity and Egg Production

From samples collected in late May and early June, sex ratios were derived and the distribution of fork length (and age) and the state of maturity was identified for both sexes. Ovaries were removed from mature females, weighed, and preserved in Davidson solution (Henderson 1963) to harden eggs and break down ovarian tissue.

Individual fecundity was calculated by subsampling ovaries by weight (Bagenal and Braum 1978). Arithmetic mean regressions were used to examine the relationships between the logarithm of fecundity and length. Male and female spring length distributions were found to be similar for all years (Chi-square $\alpha = 0.05$ based on yearly analysis of males and females in 10 size classes) so data for the two sexes were combined. Female length distributions were used to calculate mean female lengths during spawning. From the length distributions of females in each year, distributions of fecundity were derived from substitution of length distributions into fecundity versus length regressions. In years with low numbers (<10) of collected female fish (1980, 1982), a fecundity-to-length regression line from another year that had the same length–weight regression was used to estimate mean fecundity. Total fecundity was estimated by integrating the product of the length distribution and the fecundity–length relationship.

Zooplankton Abundance

Limnetic zooplankton were collected weekly or biweekly from 1981 to 1987. Samples were taken at 1, 3, 5, 8, 12, and

TABLE 1. Summary of golden shiner total abundances, age distribution, mean annual zooplankton biomass, wet weight for zooplankton, estimates of piscivore abundances, n = number of sample weeks. The perch and northern pike data for 1980–86 appear in McQueen et al. (1989).

Year	Total estimated abundance (10^3)	Estimated numbers per age-class (10^3)					Zooplankton biomass ($mg \cdot L^{-1}$) (±95% CI)	Large mouth bass estimated numbers (10^3)			Perch >10 cm (10^3)	Northern pike (10^3)
		0^+	1^+	2^+	3^+	$\geq 4^+$		Total	YOY	>YOY		
1980	21.8 (20–24)	7.9	[----------13.9----------]				—	4.9 (2.9–9.3)	3.1	1.8	4.8	0.5 (0–0.5)
1981	27.0 (25–30)	15.7	4.4	3.0	2.4	1.5	2.50±0.78 n = 10	5.9 (3.6–10.0)	3.8	2.1	12.3	0.4 (0.1–0.5)
1982	19.7 (0–31)	4.3	6.2	6.5	2.5	0.2	4.32±0.77 n = 15	1.1 (0.8–1.3)	0.1	1.0	4.2	4 captures
1983	118.9 (75–163)	94.9	6.9	[-------17.1-------]			2.49±0.77 n = 12	0.4 (0.3–0.5)	<<0.1	0.4	6.5	39 captures
1984	92.8 (87–100)	8.6	65.6	7.8	[----10.6----]		2.98±0.98 n = 8	2.8 (2.4–3.6)	2.3	0.5	2.6	0 captures
1985	77.1 (70–85)	6.5	7.4	59.1	4.1	0	4.32±0.75 n = 17	5.1 (4.7–6.6)	4.8	0.3	1.5	0.5 (0.1–0.7)
1986	44.4 (10–356)	10.0	5.2	7.6	21.6	0	2.79±0.39 n = 17	5.1 (2.0–20.5)	3.9	1.2	5.4	0.5 (0.2–5.4)
1987	22.6 (20–27)	1.4	4.6	4.9	6.0	5.7	3.01±0.63 n = 16	7.0 (4.8–10.2)	5.8	1.2	6.7	0.5 (0.3–0.9)

TABLE 2. Estimated rates of survival. Egg to 0^+ includes survival through the summer. The other survival estimates are for the entire year (fall census to fall census). The mean survival rate is based on numerically weighted annual survival rates for the entire population following the 0^+ fall census.

Year	Egg $->0^+$ (10^3)	Date	$0^+ -> 1^+$	$\geq 1^1 -> \geq 2^+$	Survival mean $n-1 -> n$
1980	0.12				
1981	0.52	1980–81	0.56	0.50	0.52
1982	0.03	1981–82	0.39	0.81	0.57
1983	1.20	1982–83	>1	>1	>1
1984	0.04	1983–84	0.69	0.77	0.71
1985	0.08	1984–85	0.86	0.75	0.76
1986	0.13	1985–86	0.80	0.41	0.45
1987	0.01	1986–87	0.46	0.48	0.48

14 m using a 35-L plexiglass trap (Schindler 1969) with 80-μm filter. The following taxonomic groups were counted: nauplii, rotifers (excluding *Asplanchna*), *Asplanchna*, *Daphnia*, *Ceriodaphnia*, *Bosmina*, and *Eubosmina*, cyclopoids and *Skistodiaptomus* and *Diaphanosoma* and a computer assisted caliper system (Sprules et al. 1981) was used to calculate zooplankton biomasses. The weekly or biweekly estimates were averaged to produce mean annual estimates.

Results

Historical Overview

Prior to 1982, the fish community of Lake St. George was dominated by bluegills (*Lepomis macrochirus*) with smaller abundances of golden shiners, yellow perch (*Perca flavescens*), pumpkinseed (*Lepomis gibbosus*), largemouth bass (*Micropterus salmoides*), rock bass (*Ambloplites rupestris*), and northern pike (*Esox lucius*) (McQueen et al. 1989). In March 1982, there was a partial winterkill. Dissolved oxygen concentrations in the lake declined to $<0.5\ mg \cdot L^{-1}$ and during ice-out, many dead fish were observed along the shoreline. The annual fish census in 1982 indicated that a substantial proportion of three of the four centrarchid populations (bluegill, largemouth bass, and rock bass, but not pumpkinseeds) were killed and that smaller portions of the yellow perch and golden shiner populations were also eliminated. In the 2 yr after the winterkill, golden shiner and yellow perch numbers rose dramatically, while centrarchid and northern pike abundances remained low. Golden shiner and yellow perch numbers declined later and centrarchid abundances, particularly largemouth bass, increased. With the exception of bluegills, census data have shown that the fish community appears to be recovering to the abundances which existed prior to the winterkill.

Golden Shiner Abundance and Survival

Prior to the winterkill (March 1982) the golden shiner population was estimated to be between 20 000 and 30 000 with approximately 50% YOY (Table 1). After the winterkill, the population was reduced by approximately 10–30% and the survival of small individuals (YOY and $0^+ \rightarrow 1+$) was low (Table 2). In 1983 YOY survival was exceptionally high (Table 2) and by the fall of 1983 the population had increased by >500%. The majority of the population comprised 0^+ indi-

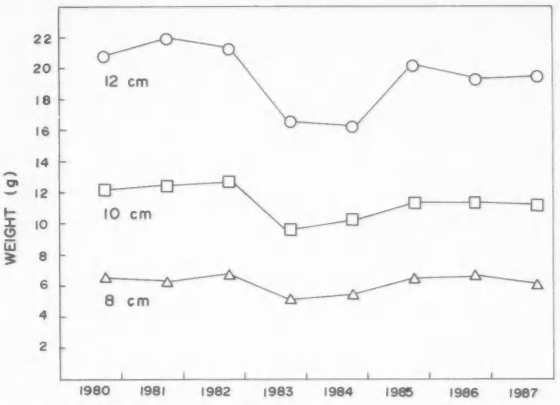

FIG. 1. Variation in the weight of 8 cm (Δ), 10 cm (□) and 12 cm (○) golden shiners during 1980–87.

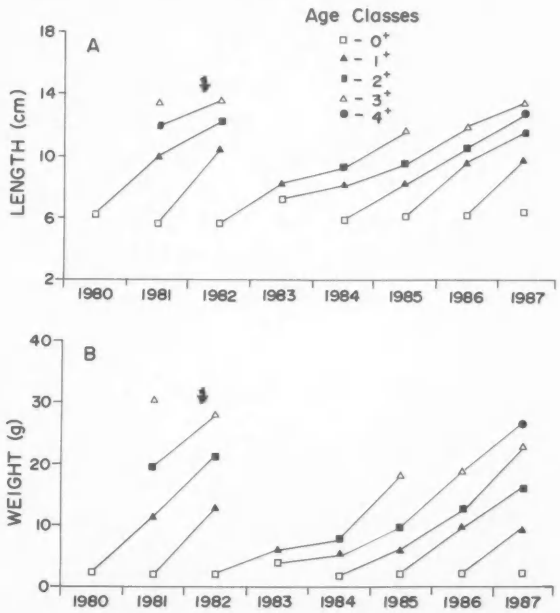

FIG. 2. Mean length (panel A) and mean weight (panel B) for ages 0^+–4^+ during 1980–87. The solid lines join the mean weights or lengths between 2 yr. Example: the 1980 year-class grew from a mean length of 6.25 cm in 1980 (0^+) to 10.14 cm in 1981 (1^+), to 12.40 cm in 1982 (2^+). The timing of the winterkill is indicated by the arrow.

viduals (Table 1) which made it difficult to obtain accurate estimates of the $>0^+$ component. This resulted in an overestimate of $>0^+$ (Table 1) and an estimate of $>0^+$ survival which exceeded 1.0 (Table 2). From 1984 through 1987, the golden shiner population was dominated by the 1983 cohort. During this period YOY survival never exceeded one-tenth of the value recorded in 1983 and the mean rate of survival for $>0^+$ individuals decreased during 1986 and 1987.

Golden Shiner Length–Weight Relationships

Length–weight regression lines for 1982 and 1985, were equal with greater slopes and elevations than all other years ($\alpha = 0.05$). The 1980, 1981, 1986, and 1987 relationships were all equal ($\alpha = 0.05$) with intermediate slopes and elevations. The 1983 and 1984 relationships were equal ($\alpha = 0.05$) with smaller slopes and elevations than in other years. These data suggest that when golden shiner abundances were greatest (1983, 1984), weight at length was significantly reduced (Fig. 1).

Golden Shiner Growth

Golden shiner mean lengths (Fig. 2A) and mean weights (Fig. 2B) at age varied together between 1980 and 1987. For older golden shiners (1^+ to 3^+), both mean lengths and weights increased in 1982 after the winterkill, decreased in 1983 and 1984 and increased in 1985, 1986, and 1987 (ANOVA, $\alpha = 0.05$). For seven of the eight years included in this study, there was no difference in YOY length or weight at the first fall census (Fig. 2, Student Newman–Keuls $\alpha = 0.05$). The exception was 1983, when both length and weight were higher. During ths year egg to 0^+ survival was exceptionally high (Table 2) and recruitment was the highest recorded (Table 1).

Golden Shiner Fecundity

The four-fold increase in female abundance in 1984 and 1985 and the decrease in mean length (Table 2) resulted from the maturation of the 1983 year-class into an adult population. Estimates of total egg production from 1980 to 1987 showed a seven-fold difference between low and high values (Table 3). The highest total egg production was found in 1984 and was associated with the large abundance of mature females in that year, but this did not translate into any clearly defined stock–recruitment relationship (Fig. 3).

Zooplankton Abundance

Mean total zooplankton biomass in Lake St. George, from 1981 to 1987, ranged from 2.49 to 4.32 $mg \cdot L^{-1}$ wet weight (Table 1). An ANOVA, followed by a Student Newman–Keuls multiple range test, indicated that during 1982, mean zooplankton biomass rose significantly ($\alpha = 0.05$) from levels recorded in 1981 and then decreased in 1983 and 1984 ($\alpha = 0.05$) and then increased in 1985 ($\alpha = 0.05$).

Zooplankton Abundance and Golden Shiner Condition, Growth, and Abundance

There was a significant positive relationship between total golden shiner condition factor and zooplankton biomass (Table 4), but there were no significant relationships between zooplankton biomass and YOY golden shiner condition factor or length. There were also no significant relationships between mean annual zooplankton biomass and egg to 0^+ survival or $>0^+$ mean survival (Table 4). For both data sets, 1983 stands out as a year with exceptionally high rates of survival, but zooplankton biomass was among the lowest recorded.

Piscivore Abundance

The Lake St. George piscivore population (Table 1) comprised largemouth bass and northern pike (primary piscivores) and yellow perch >10 cm (secondary piscivores). Before the winterkill, piscivore abundance was high. During the winterkill, piscivore numbers declined by >70%. After the winterkill, numbers gradually increased so that by 1987, the numbers

TABLE 3. Summary of reproductive data for golden shiners in Lake St. George: year, mature female abundance, percent mature females (n = number of females observed for the sex ratio estimate), mean female length (±95% CI), mean fecundity (±95% CI), total egg production.

Year	Mature female abundance	Percent mature females[a] (n)	Mean female length (cm)	Mean fecundity (eggs/female)	Total egg production (10^6)
1980	3876 (730–7701)	55 (40)	11.75 (±1.03)	1763 (±537)	6.84[c]
1981	5822 (3660–8436)	50[b] (11)	10.08 (±0.32)	588 (±89)	2.99
1982	10 337 (8370–12 606)	49 (51)	11.80 (±0.33)	1558 (±228)	16.10[d]
1983	7575 (5864–9528)	50[b] (13)	10.32 (±1.05)	1133 (±269)	7.92
1984	25 955 (23 515–29 040)	47 (148)	9.18 (±0.18)	856 (±172)	22.22
1985	23 407 (21 322–25 690)	55 (277)	8.60 (±0.40)	334 (±23)	7.92
1986	12 404 (11 172–13 941)	55 (51)	10.71 (±0.55)	642 (±95)	7.97
1987	6859 (4858–9685)	48 (599)	11.59 (±0.18)	2133 (±122)	14.63

[a]Chi-square analysis ($p < 0.01$) between 1980, 1982, 1984, and 1987 indicated that sex ratio was 50:50.

[b]Low sample size, sex ratio assumed to be 50:50.

[c]Low number of fecundity estimates (<10), 1986 fecundity to length regression used to estimate fecundity.

[d]Low number of fecundity estimates (<10), 1985 fecundity to length regression used to estimate fecundity.

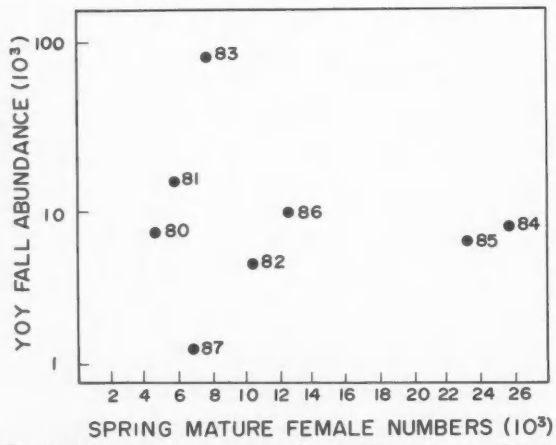

FIG. 3. Relationship between the spring abundance of mature female golden shiners and the fall abundance of YOY golden shiners during 1980–87.

approximated prewinterkill abundances. In most years, largemouth bass comprised a significant portion of the predator population, but during the winterkill, the largemouth bass population was reduced by >500% and recruitment of YOY bass during 1982 and 1983 was low (6 and 1%, respectively) relative to other years. During 1984, YOY bass again became the largest portion (82%) of the population. Recruitment was high in 1985 (95%), 1986 (76%), and 1987 (83%) and bass abundances reached levels similar to those observed before the winterkill.

TABLE 4. Summary of correlation coefficients relating mean annual zooplankton biomass to golden shiner length, condition, and survival. NS = not significant at $p < 0.05$, S = significant at $p < 0.05$.

Zooplankton biomass correlated with the variables	r	Two tailed probability	Number of years
Total golden shiner condition factor	+0.79	S	7
YOY golden shiner condition factor	+0.19	NS	7
Mean YOY length in the fall	−0.42	NS	7
Egg to 0^+ fall survival	−0.55	NS	7
Mean annual golden shiner survival	−0.02	NS	7

Piscivore Abundance and Golden Shiner Abundance

The relationships between mean annual golden shiner survival from year $n-1 \rightarrow n$ and piscivore abundances estimated in year n were all negative (Table 5) the strongest relationship was between mean annual golden shiner survival and the abundance of bass older than 0^+ (Fig. 4).

Discussion

The winterkill at Lake St. George selectively removed many of the piscivores and some of the planktivores. During the

TABLE 5. Summary of correlation coefficients relating measures of golden shiner annual survival to estimates of predator abundance.

First variable	Second variable	r	Two tailed probability	Number of years
Total piscivore number	Mean annual golden shiner survival	−0.56	$p < 0.10$	7
Total largemouth bass	Mean annual golden shiner survival	−0.67	$p < 0.05$	7
Largemouth bass > YOY	Mean annual golden shiner survival	−0.73	$p < 0.03$	7

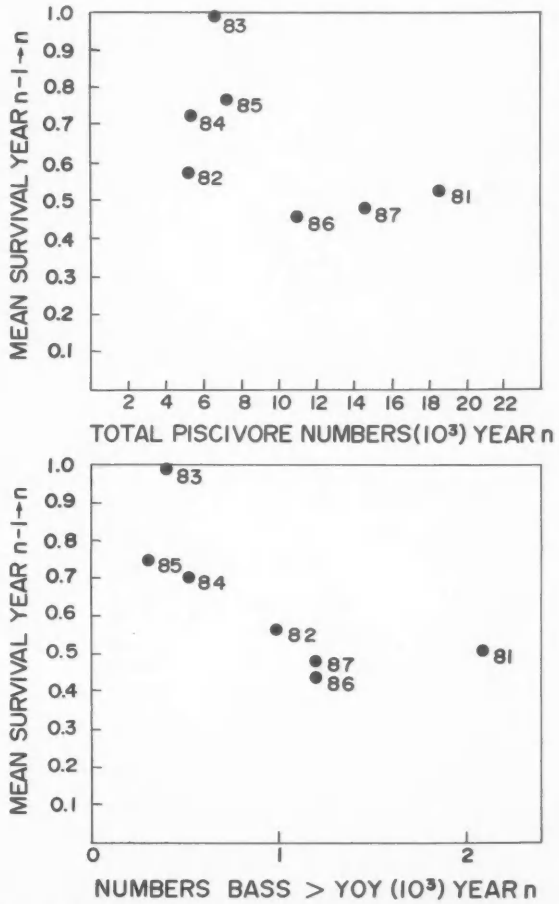

FIG. 4. Top panel: the relationship between mean annual golden shiner survival (Table 2) from year $n-1 \rightarrow n$ and total piscivore numbers in year n. Bottom panel: the relationship between mean annual golden shiner survival (Table 2) from year $n-1 \rightarrow n$ and number of bass >YOY in year n.

recovery phase (1982–87) zooplankton abundance was also strongly affected (McQueen et al. 1989). These changes in community structure provided an opportunity to evaluate the relative influences of food availability and predators on golden shiner abundance.

TABLE 6. Mean lengths (±95% CI) for YOY golden shiners and largemouth bass measured in September of each year. The sample sizes are included in parentheses.

Year	YOY golden shiners	YOY largemouth bass
1980	6.26±0.49 (n = 23)	7.13±0.16 (n = 465)
1981	5.80±0.61 (n = 43)	7.16±0.02 (n = 582)
1982	5.77±0.34 (n = 42)	—
1983	7.26±0.76 (n = 62)	—
1984	5.81±0.73 (n = 77)	6.40±0.19 (n = 59)
1985	6.08±0.89 (n = 58)	6.53±0.04 (n = 115)
1986	6.24±0.14 (n = 37)	7.26±0.55 (n = 50)
1987	6.58±0.31 (n = 16)	7.24±0.19 (n = 198)

Influence of Food Abundance

We investigated two potential relationships between food availability and golden shiner abundance. First, we hypothesized that food quantity could indirectly influence fish abundance through altered golden shiner growth and that this in turn could result in size-related differences in fecundity. Tests of this hypothesis suggested that: (1) the condition factor for the entire golden shiner population was positively related to food abundance (Table 4), (2) female length (Table 3) was important in determining the annual estimated egg production, but (3) there was no relationship between estimated egg production and YOY fall recruitment (Table 2, 3), or (4) between numbers of mature females and YOY recruitment. Forney (1957) drew similar conclusions from studies of bass–shiner ponds. Our second hypothesis was that food abundance could directly influence golden shiner abundance through altered survival. Tests of this hypothesis (Table 4) suggested that there were no correlations between zooplankton abundance and (1) 0^+ condition, (2) egg to 0^+ survival or (3) mean annual golden shiner survival. Together, these results suggest that zooplankton abundance appears to have had little indirect or direct influence on golden shiner recruitment and abundance.

Influence of Predators

All of the correlations between predator numbers and mean annual golden shiner survival (for fish older than 0^+) were negative and the highest correlation coefficient was obtained for golden shiner survival and >YOY largemouth bass (Table 5). This relationship appears to derive from the relative reproductive lags and growth rates for golden shiners and largemouth bass. During the winterkill year (1982), YOY recruitment was low for both populations (Table 1). During 1983, golden shiner YOY recruitment was very high (Table 1), but largemouth bass recruitment was still low (Table 1). After 1984, the large golden shiner cohort from 1983 dominated the age distribution and mean annual golden shiner survival values were high during both 1984 and 1985 (Fig. 4). After 1984, the largemouth bass began to recruit, but it was not until 1986 and 1987 that individual bass were large enough to consume the adult golden shiners from the 1983 cohort. This resulted in a 1986–87 reduction (approximately 40%) in golden shiner survival (Fig. 4), and in a rapid decline in the overall golden shiner population size (Table 1).

A number of published accounts suggest that YOY predators can have significant negative impacts on the recruitment of YOY prey (e.g. alewives, Crowder 1980; Stewart et al. 1981; Mansfield and Jude 1986; yellow perch, Bagenal 1977; Nielsen 1980; Mills et al. 1987a; shad, Farquhar et al. 1980; Storck 1986;

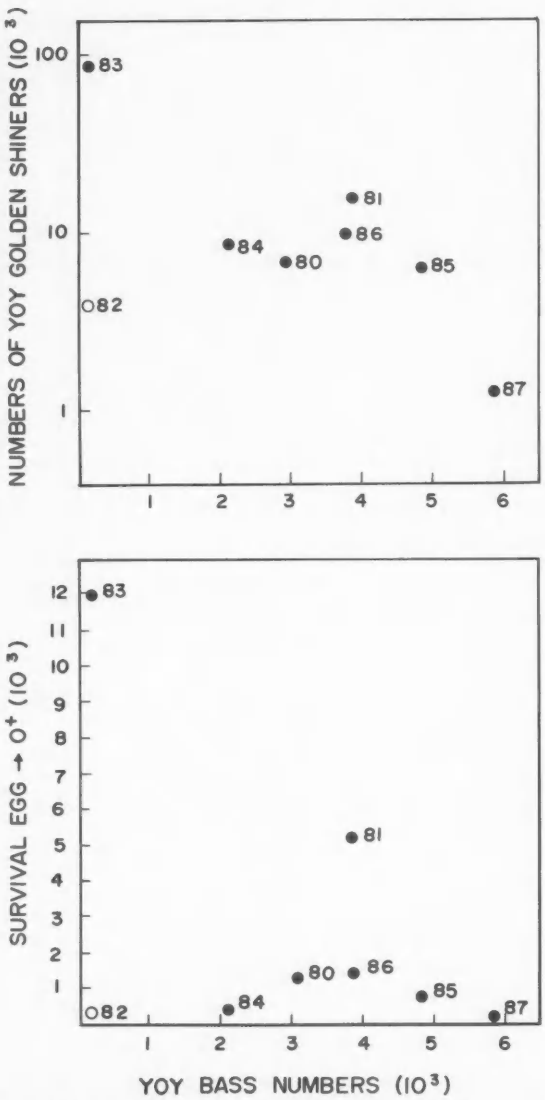

FIG. 5. Top panel: abundance of YOY golden shiners ($\log_{10}$ scale) plotted with respect to numbers of YOY largemouth bass. Bottom panel: survival from egg to 0^+ (fall census) plotted with respect to numbers of YOY largemouth bass.

Adams and DeAngelis 1987 and bloaters, Rice et al. 1987). Lawrence (1957) has shown that golden shiners that are up to 60–70% of the size of small bass are vulnerable to predation. At Lake St. George, YOY largemouth bass lengths (Table 6) measured in the fall of each year were greater than the lengths of YOY golden shiners. Because the bass entered the water column before the shiners and because the fall length data were biased by the removal of small more vulnerable shiners, it seems probable that most YOY golden shiners were vulnerable to YOY bass for most of the summer during all years. Together, these results suggest that predation by YOY largemouth bass on YOY golden shiners was possible and correlation analysis shows that there is a negative relationship ($r = -0.57, p < 0.08$) between fall standing stocks of YOY largemouth bass and YOY golden shiners (Fig. 5). This general trend is supported by a negative relationship between YOY largemouth bass numbers and YOY shiner egg to fall 0^+ survival (Fig. 5), but the dominance of the 1983 YOY survival value makes statistical analysis questionable.

We found several significant negative relationships between golden shiner abundance and recruitment and the abundance of piscivores. These results are in general agreement with the results obtained by Tonn and Paszkowski (1986) who showed that size-dependent predation by yellow perch was the primary factor that determined the density and size structure of mudminnow (*Umbra limi*) populations. Also, Carpenter et al. (1985) and McQueen et al. (1986) have both hypothesized a strong influence of piscivores on planktivores. Carpenter et al. (1985) speculated that a winterkill might be expected to selectively remove the larger fish (typically piscivores) which should result in increased abundances of planktivores. The slow recovery of piscivores would be expected to allow planktivore abundances to remain high until strong recruitment could reestablish piscivore abundances to prewinterkill levels. These are the general patterns that are suggested by the Lake St. George data set, and we conclude that predator abundance is strongly implicated in the regulation of golden shiner numbers.

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A Conditional Generalized Least Squares Method for Estimating the Size of a Closed Population[1]

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In the corrected Leslie–DeLury catch-per-unit-effort method, estimation of the corrected cumulative catches causes the underlying model to be an errors-in-covariates structural model with a nondiagonal dispersion matrix. This violates the assumptions of regression and causes the corrected Leslie–DeLury method to give biased estimates of the population size and its variance. We use generalized least squares and a controlled variables design to resolve these difficulties, obtain the minimum-variance unbiased linear estimator, and compute unbiased variance estimates. We apply our method to sockeye salmon fingerlings (*Oncorhynchus nerka*) netted in a hatchery pond. For these data, arranged according to the controlled variables design, the corrected Leslie–DeLury method underestimates the standard error of the population size by 41%.

Dans la méthode corrigée des captures par unité d'effort de Leslie–DeLury, le calcul des prises cumulatives corrigées se traduit par des erreurs dans le modèle structural de covariables dans une matrice de dispersion non diagonale. Ce phénomène va à l'encontre des hypothèses de régression et la méthode corrigée de Leslie–DeLury donne ainsi des estimations biaisées de la taille de la population et de sa variance. Nous avons utilisé les moindres carrés généralisés et un système de variables contrôlées pour résoudre ces problèmes, obtenir une méthode d'estimation linéaire non biaisée présentant la variance la moindre, et en arriver à des estimations non biaisées de la variance. Nous appliquons notre méthode aux tacons de saumon sockeye (*Oncorhynchus nerka*) capturés dans une écloserie. Dans le cas de ces données, arrangées selon le système de variables contrôlées, la méthode corrigée de Leslie–DeLury sous-estime l'erreur type de l'effectif de 41%.

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The use of catch-per-unit-effort (CPUE) to estimate the size of a closed population was introduced by Leslie and Davis (1939), and the derivation of the method was provided by DeLury (1951) and Chapman (1954). Chapman (1961) and Paloheimo (1961) suggested an approximate correction for the bias in the CPUE within sampling intervals, and Braaten (1969) demonstrated that this correction reduces the mean squared error. (D. G. Chapman, University of Washington, Seattle, WA, pers. comm.) suggested calling the resulting procedure the "corrected Leslie–DeLury method." Reviews of CPUE methods are presented by Ricker (1975) and Seber (1982).

The corrected Leslie–DeLury method is based upon linear regression of the CPUE's upon the corrected cumulative catches. Three of the assumptions underlying linear regression are that the errors are independent and identically distributed and the independent variable is measured exactly. However, when the corrected cumulative catches are estimated from catch and effort data two of these assumptions are violated: (1) the independent variable is measured with error, and (2) as a consequence of the cumulative nature of the independent variable, the errors from the regression line are not independent. The third assumption is violated because as Zippin (1956), Ricker (1975), Seber (1982), Crittenden (1983), and others pointed out, CPUE's are usually heteroscedastic and hence the errors are not identically distributed.

We show below that these violations of the assumptions underlying the corrected Leslie–DeLury method cause it to be an errors-in-covariates structural model which has a misspecified dispersion matrix. When linear regression, which is used to obtain the corrected Leslie–DeLury estimate, is applied to an errors-in-covariates structural model, the regression coefficients are well known to be biased (Moran 1971; Seber 1977; Hodges and Moore 1972; Davies and Hutton 1975; and others); and even if the model were of a type to which simple linear regression could be validly applied, the misspecification of the dispersion matrix would cause the coefficient estimates to be not minimum variance and their variances to be biased. In this paper we present a method which resolves these difficulties and apply it to catch effort data on sockeye salmon (*Oncorhynchus nerka*) fingerlings netted in a hatchery pond.

Methods

Our method is a generalized least squares estimate based on a controlled variables model. Generalized least squares can be

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TABLE 1. Notation.

Symbol	Meaning
A	Matrix defining the linear transformation $e = AU$
B	Matrix describing the covariation between CPUE and K
C	Catch
CPUE	Catch-per-unit-effort
e	Random error in (10)
f	Effort
K	Corrected cumulative catch
M	Number of sampling units in the statistical population
m	Number of units sampled
N_c	School size
N_i	Population size at the beginning of interval i
n	Number of intervals
q	Catchability
U	Vector of ε's followed by δ's
w	Statistical weight
β_i	Regression coefficient
δ_i	Error component in K_i
ε_i	Error component in (9)

used to obtain the minimum variance unbiased linear estimate and unbiased variance estimates when the dispersion matrix is known (Seber 1977; Draper and Smith 1981), and we present a method for estimating the dispersion matrix. Since the dispersion matrix is estimated rather than being known, our estimator is an "estimated generalized least squares estimator." The properties of this type of estimator differ slightly from those of generalized least squares estimators and are reviewed by Judge et al. (1982). However, since the estimation error in the dispersion matrix should be small in this application for moderate or large sample sizes, we discuss our method as if the dispersion matrix is known.

We use a controlled variables design because conditional regression applied to this type of data yields unbiased estimates even if the independent variable is measured with error (Berkson 1950). Thus, by using Berkson's controlled variables model we circumvent the difficulty of errors in covariates and by using conditional generalized least squares we account for the nondiagonal dispersion matrix.

We also employ a conditional regression to estimate the CPUE for each interval. Corrected cumulative catches are computed using these estimated CPUE's and together the CPUE's and the corrected cumulative catches provide the data set used in the above controlled variables regression model. The essential feature of the controlled variables design is that the independent variables have predetermined fixed values. Hence, we adjust the boundaries of the intervals so that the total catch from each interval has a fixed value.

We develop our method for the analysis of the same type of catch–effort data as the corrected Leslie–DeLury method. These are data which come from a sampling design where the captures occur at random from a closed population (a population for which there is no mortality, no recruitment, no emigration, and no immigration, but from which catches are taken over several intervals), where there is no interference among units of effort, the gear units are equally efficient, all the fish in the population have an equal probability of capture, and the catches are small relative to the size of the fish population. Braaten (1969) showed that use of the correction to the cumulative catch allows larger catches to be considered, and Crittenden (1983) introduced a weighting which allows the assumption that the probability of capture is constant to be replaced by the assumption that it is an identically distributed random variable and which also accounts for the capture of schools of fish.

We consider the design where there are M_i sampling units in n consecutive time intervals and m_i of these units are sampled for catch and effort. In the fingerling example each sampling unit is a net haul, but in other applications it could be a boat, a person, or any of a large number of possible alternative units. The M_i's and m_i's are adjusted so that the estimated total catch from each interval has a fixed value, and these values are set before the data set is taken. Notation is given in Table 1.

The first step is to estimate the CPUE and its variance for each of the n time intervals. Smith (1980) and Quinn et al. (1982) discuss several estimation methods including weighted linear (conditional) regression. We selected that method because, as Seber (1977) and Draper and Smith (1981) pointed out, it gives estimates which are asymptotically normal, minimum variance, linear, and unbiased when the weights are selected so that they stabilize the variance and the independent variable is measured without error. Approximate normality is advantageous in the next step, where we apply generalized least squares, because when the data pass the tests for normality, the familiar tests and diagnostics associated with regression can be used.

Seber (1977) and Draper and Smith (1981) showed that weighting will stabilize the variance if the weights are proportional to the reciprocal of the variances and the corresponding variance stabilizing transformation is done by multiplying both sides of the regression model by the square root of the weight.

Zippin (1956) suggested a weighting based on the assumptions that the variance of the catch is proportional to the expected catch and that the expected catch for each unit is proportional to the effort. Such a variance structure will result from a Poisson distribution, and occurs when capture is a rare, independent event with constant probability. However, Ricker (1975) pointed out that variation in the catches is often due more to random variation in the catchability than to Poisson variation and, consequently, Zippin's (1956) method often does not adequately stabilize the variance.

Crittenden (1983) showed that when the catchability q is a random variable and fish are caught in schools of size N_c, the variance of the catch is a quadratic polynomial of the expected catch, $\mathrm{Var}(C_{i,j}) = N_c(EC_{i,j}) + CV(q)^2(EC_{i,j})^2$, where $CV(q) = SE(q)/\bar{q}$ is the coefficient of variation of the catchability, C is the catch, i designates the interval and j designates the unit. This relationship implies that weights should be selected based on the ratio of the square of the coefficient of variation of the catchability to the school size. Specifically, if $CV(q)^2/N_c << 1$, the variance of the catch will be a linear function, which leads to Zippin's (1956) weighting; if $CV(q)^2/N_c >> 1$, it will be a squared function; and otherwise, it will be a quadratic polynomial which does not have a constant term. Although $CV(q)$ and N_c will usually be unknown, this result suggests a family of alternative weights.

The CPUE and its variance can be estimated in each interval using weighted linear regression forced through the origin based on the model,

$$(1)\quad C_{i,j}|f_{i,j} = \beta_i f_{i,j} + e_{i,j},$$

where f is the effort and $\hat{\beta}_i = \widehat{\mathrm{CPUE}}_i$ is the estimated slope and is an estimate of CPUE_i. This regression model (1) is conditional upon the observed efforts, which may exhibit random variation but are assumed to be measured without error. The CPUE's can either be estimated using n separate regressions

based on (1) or these regressions may be combined by using effect coding for the intervals. Forthofer and Lehnen (1981) review coding methods.

Accounting for Confounding Variables

Day to day variation in the catch can be caused by variation in an unmeasured variable which influences the catchability. Examples of such confounding variables include weather conditions, water clarity, time of day, the gear type, and many other possible variables. DeLury (1951) pointed out that if variation due to a confounding variable is random it can be treated as random error but not trends throughout the data.

When random variation in the confounding variable is expressed as variation among sampling units, the resulting variability will increase the coefficient of variation of the catchability and Crittenden's (1983) method will automatically incorporate it into the estimate. In contrast, when variation due to the confounding variable is expressed as random variation among intervals, Crittenden's method will not account for its effects. Random variation among intervals will increase the scatter about the regression model and will be reflected in the value of $\hat{\sigma}^2$. As this decreases the accuracy with which the methods we present below allow us to specify the dispersion matrix, a preferable approach would be to use a sampling design in which variation in suspected confounding variables occurs among units rather than among intervals.

When variation in the confounder is not random with respect to the cumulative catch, but occurs in a trend, underspecification bias results. Seber (1977) and Draper and Smith (1981) pointed out that underspecification bias can be avoided by identifying and measuring the confounding variable and including it in the model using multiple regression. This approach will also resolve the difficulties due to random variation among intervals.

CPUE and Total Catch both Conditional on N_i

The catches taken during any one interval are from a population whose size at the beginning of that interval is fixed (although unknown), that is, the observed catches are conditional upon the realized population size at the beginning of the interval, N_i. This also applies to the estimated CPUE and the estimated total catch from the interval. The conditional total catch can be estimated using the equation.

$$(2)\quad \hat{C}_i|N_i = (M_i - m_i)\bar{f}_i\, \hat{\text{CPUE}}_i|N_i + \Sigma_{j=1}^{m} C_{i,j},$$

where $\bar{f}_i$ is the mean effort and $\hat{\text{CPUE}}_i|N_i$ is the slope from (1). Equation (2) is used to adjust M_i and m_i so that $\hat{C}_i|N_i$ has a predetermined fixed value. This restricts our method to experimental designs where this reassignment of the interval boundaries is valid.

Because of the difficulty in establishing the exactly correct weights for (1), we estimate $\text{Var}(\hat{\text{CPUE}}_i|N_i)$, $\text{Var}(\hat{C}_i|N_i)$ and $\text{Cov}(\hat{\text{CPUE}}_i|N_i, \hat{C}_i|N_i)$ using the bootstrap resampling technique (Efron 1982; Efron and Tibshirani 1986). When an incorrect weighting is used in (1) the regression coefficients $\hat{\beta}_i = \hat{\text{CPUE}}_i$ will be unbiased but will not be minimum variance and the variance estimates obtained analytically from regression will be biased (Seber 1977; Draper and Smith 1981). Consequently, we obtain the vector $\hat{\text{CPUE}}^T = (\hat{\text{CPUE}}_1, \hat{\text{CPUE}}_2, \ldots, \hat{\text{CPUE}}_n)$ analytically from (1) but we use a bootstrap resampling technique to obtain its dispersion matrix Var(CPUE), where Var(CPUE) is the n by n diagonal matrix with elements $\text{Var}(\hat{\text{CPUE}})_{i,j} = \text{Var}(\hat{\text{CPUE}}_i)$. Using this approach, incorrect weighting only decreases the accuracy of the estimated CPUE's, and the variance estimates remain reliable. The covariance $\text{Cov}(\hat{\text{CPUE}}_i|N_i, \hat{C}_i|N_i)$ also needs to be computed, since the mean is not independent of the slope for regression forced through the origin, which is the type of model in (1).

To estimate these variances and the covariance using the bootstrap, resample with replacement from the m_i data points $(C_{i,j}, f_{i,j})$ to form m_i new observations, based on this new data set compute the weighted regression (1) and compute $\hat{C}_i|N_i$ using (2) but with $\Sigma_{j=1}^{m} C_{i,j}$ computed using the original data set. This procedure is repeated many times, each time storing $\hat{\text{CPUE}}_i|N_i$ and $\hat{C}_i|N_i$. The sample estimates of $\text{Var}(\hat{\text{CPUE}}_i|N_i)$, $\text{Var}(\hat{C}_i|N_i)$ and $\text{Cov}(\hat{\text{CPUE}}_i|N_i, \hat{C}_i|N_i)$ based on the stored values of $\hat{\text{CPUE}}_i|N_i$ and $\hat{C}_i|N_i$ are the bootstrap variances and covariance.

Corrected Cumulative Catch

The corrected cumulative catch is $K_i \equiv C_i/2 + \Sigma_{j=1}^{i-1} C_j$ conditional on N_k for $(k = 1,2,\ldots,i)$ and is obtained using the equation

$$(3)\quad \hat{K}_i|N_{1,2,\ldots,i} = (\hat{C}_i|N_i)/2 + \Sigma_{k=1}^{i-1}(\hat{C}_k|N_k).$$

From here onwards in the paper everything is conditional upon $N_1, N_2, \ldots, N_n$ but we omit the conditional statement in the equations to simplify the notation. The variance of the conditional corrected cumulative catch is

$$(4)\quad \text{Var}(\hat{K}_i) = \text{Var}(\hat{C}_i)/4 + \Sigma_{k=1}^{i-1}(\text{Var}(\hat{C}_k))$$

and its covariances are

$$(5)\quad \text{Cov}(\hat{K}_i, \hat{K}_{k<i}) = \text{Var}(\hat{K}_k),$$

$$(6)\quad \text{Cov}(\hat{\text{CPUE}}_i, \hat{K}_i) = \text{Cov}(\hat{\text{CPUE}}_i, \hat{C}_i)/2,$$

$$(7)\quad \text{Cov}(\hat{\text{CPUE}}_i, \hat{K}_{k>i}) = \text{Cov}(\hat{\text{CPUE}}_i, \hat{C}_i), \text{ and}$$

$$(8)\quad \text{Cov}(\hat{\text{CPUE}}_i, \hat{K}_{k<i}) = 0.$$

We use the vector $\hat{K}^T = (\hat{K}_1, \hat{K}_2, \ldots, \hat{K}_n)$ and its dispersion matrix $\text{Var}(\hat{K})$, below in (11). This matrix is the n by n symmetric matrix with diagonal elements $\text{Var}(\hat{K})_{i,i} = \text{Var}(\hat{K}_i)$ computed using (4) and with off-diagonal elements $\text{Var}(\hat{K})_{i,k\neq i} = \text{Cov}(\hat{K}_i, \hat{K}_k)$ computed using (5). The vector $\hat{K}$ is easily computed using the matrix equation $\hat{K} = G\hat{C}$ where $\hat{C}^T = (\hat{C}_1, \hat{C}_2, \ldots, \hat{C}_n)$ and G is the n by n matrix with one-half's on the diagonal, zeros above the diagonal, and one's below the diagonal. The variance of $\hat{K}$ can be obtained using the equation $\text{Var}(\hat{K}) = G\text{Var}(\hat{C})G^T$.

We also use the n by n matrix B which describes the covariation of CPUE and K. The matrix B has diagonal elements $B_{i,i} = \text{Cov}(\hat{\text{CPUE}}_i, \hat{K}_i)$ computed using (6), elements $B_{i,k>i} = \text{Cov}(\hat{\text{CPUE}}_i, \hat{K}_{k>i})$ computed using (7), and zeros below the main diagonal $B_{i,k<i} = 0$, based on (8).

Conditional Regression Model

Based on Baranov's (1918) catch equation and Chapman's (1961) and Paloheimo's (1961) approximation that the average abundance during interval i is $N_i - K_i$, the conditional CPUE can be expressed using the linear model

$$(9)\quad \hat{\text{CPUE}}_i = N_1 q - q K_i + \epsilon_i$$

for known values of K_i and where ϵ_i's are the error components. Equation (9) is a "structural model" rather than a "functional model" because it is based on a law-like relationship between

the realized values of mathematical variables rather than between their expectations (Seber 1977; Moran 1971).

When the K_i's are estimated rather than being known, K_i in (9) should be replaced by $K_i = \hat{K}_i + \delta_i$ where $\hat{K}_i$ and δ_i are random variables and are correlated. In matrix notation (9) becomes

$$(10) \quad Y = X\beta + e$$

where Y is a column vector with elements $Y_i = \text{CPUE}_i$, X is the n by 2 design matrix which has ones in the first column and elements $X_{i,2} = \hat{K}_i$ in the second column, β is the two element column vector where $\beta^T = (\beta_0 = N_1 q, \beta_1 = -q)$, and e is the n element column vector of error components with elements $e_i = \epsilon_i - q\delta_i$. This is an "errors-in-covariates structural model" and the estimate $\beta_\Delta = (X^T\text{Var}(e)^{-1}X)^{-1}X^T\text{Var}(e)^{-1}Y$ (Seber 1977; Draper and Smith 1981) obtained by applying generalized least squares conditionally to (10) is well known to be biased because $E(\beta_\Delta) = E[(X^T\text{Var}(e)^{-1}X)^{-1}X^T\text{Var}(e)^{-1}(X - q\delta)\beta] = \beta - b$ where the bias is $b = (X^T\text{Var}(e)^{-1}X)^{-1}X^T\text{Var}(e)^{-1}q\delta\beta$ and $b \neq 0$ since X and δ are both random variables and are correlated (Moran 1971; Seber 1977; Hodges and Moore 1972; Davies and Hutton 1975, and others).

We avoid this difficulty by using Berkson's (1950) "controlled variables" approach: if the measured values of the independent variable are preset constants, then K_i and δ_i are random variables, $\hat{K}_i$ is a fixed constant, and the estimate is unbiased since $E(\beta) = E[(X^T\text{Var}(e)^{-1}X)^{-1}X^T\text{Var}(e)^{-1}(X - q\delta)\beta] = \beta$ because X is constant and $E\delta = 0$. In order to compute these generalized least squares estimates the dispersion matrix Var(e) needs to be estimated.

Generalized Least Squares

To estimate Var(e) we define the vector $U^T \equiv (\epsilon_1, \epsilon_2, \ldots, \epsilon_n, \delta_1, \delta_2, \ldots, \delta_n)$. The vector e is related to U by the linear transformation $e = AU$ where $A = [I_n, -qI_n]$ is the n by $2n$ matrix in two blocks where the first block is the identity matrix of size n and the second block is $-q$ times the identity matrix of size n. The variance of the vector e is obtained using the equation $\text{Var}(e) = A\text{Var}(U)A^T$ where Var(U) is the $2n$ by $2n$ matrix in four blocks.

$$(11) \quad \text{Var}(U) = \begin{bmatrix} \text{Var}(\hat{\text{CPUE}}) & B \\ B^T & \text{Var}(\hat{K}) \end{bmatrix},$$

where equations for the matrices Var(CPUE), B, and Var($\hat{K}$) are given above.

In generalized least squares (reviewed by Seber 1977; Draper and Smith 1981), nonindependence and heteroscedasticity are corrected by premultiplying the linear model by the inverse of the square root of the dispersion matrix, to give the transformed model,

$$(12) \quad \text{Var}(e)^{-1/2}Y = \text{Var}(e)^{-1/2}X\beta + \text{Var}(e)^{-1/2}e,$$

in which $\text{Var}(e)^{-1/2}e$ is independently and identically distributed, is asymptotically normal, and has a mean of zero and dispersion matrix $\sigma^2 I$. This is a regression with no constant upon the two variables given by the two columns of $\text{Var}(e)^{-1/2}X$. The regression coefficients retain their definitions from the untransformed model (Seber 1977; Draper and Smith 1981), and for this application, these definitions are $\beta_0 = N_1 q$ and $\beta_1 = -q$. Residual plots and tests of normality should be done using $\text{Var}(e)^{-1/2}(Y - X\hat{\beta})$. The inverse square root matrix $\text{Var}(e)^{-1/2}$ can be obtained using the equation $\text{Var}(e)^{-1/2} = Q\Lambda^{1/2}Q^T$ where Q is the matrix of eigenvectors of $\text{Var}(e)^{-1}$ and Λ is the corresponding diagonal matrix of eigenvalues (Strang 1980). Westlake (1968) reviews several alternative methods for finding the square root matrix.

Generalized least squares regression is not currently available in many statistical computer packages. However, the computations are simple using a statistical package which provides matrix arithmetic. With such a package, one can either conduct generalized least squares by matrix manipulations using the equations presented by Seber (1977) and Draper and Smith (1981) or transform the model and apply ordinary linear regression based on (12). The latter approach has the advantage that it provides easy access to the diagnostics, tests, and graphics that usually are included in regression packages.

Abundance Estimation

Although the coefficient estimates are unbiased, the inverse regression used to obtain the abundance estimate $\hat{N}_1 = -\hat{\beta}_0/\hat{\beta}_1$ is a nonlinear transformation and therefore gives a biased estimate. We correct this bias by employing the delta method

$$(13) \quad E(\hat{N}_1) = -\hat{\beta}_0/\hat{\beta}_1 - \hat{\beta}_0\text{Var}(\hat{\beta}_1)/\hat{\beta}_1^3 + \text{Cov}(\hat{\beta}_0, \hat{\beta}_1)/\hat{\beta}_1^{-2},$$

where $\text{Cov}(\hat{\beta}_0, \hat{\beta}_1)$ is $\hat{\sigma}^2$ times the off-diagonal element of the two by two symmetric matrix $(X^T\text{Var}(e)^{-1}X)^{-1}$. The variance of $\hat{N}_1$ is approximated using the equation

$$(14) \quad \text{Var}(\hat{N}_1) = \hat{\beta}_1^{-2}\text{Var}(\hat{\beta}_0) + \hat{\beta}_0^2\text{Var}(\hat{\beta}_1)/\hat{\beta}_1^4 - 2\beta_0\text{Cov}(\hat{\beta}_0, \hat{\beta}_1)/\hat{\beta}_1^3.$$

Data and Results

These methods are illustrated using data on salmon fingerlings (*Oncorhynchus nerka*) dip-netted from a hatchery pond (Table 2). There are $n = 6$ intervals and net hauls are the sampling unit. Effort is the volume sampled. The pond was stratified into three regions, near the inlet, the central region, and near the outlet. Although the fingerlings had all been raised together and were of the same age and origin, some were larger and more active, and the fingerlings near the inlet appeared to be predominately those individuals. Consequently, stratification was used to remove this source of variation, and each haul consists of several dips with equal representation from each strata. Resting invervals were allowed between hauls to allow the fish to recover. To reduce bias and avoidance, netting was done by reaching out from behind the pond's retaining wall, so that the fingerlings and the operator could not see each other.

Calculations were done in the Minitab statistical package. CPUE were computed using a linear regression with effect coding. Zippin's (1956) weighting was used because the uniformity of the size and condition of the fingerlings and the stratified sampling design resulted in there being little variation in the catchability, and residual plots indicate that Zippin's (1956) weighting stabilizes the variance. The number of sampling units in each interval are adjusted so that the total catches are fixed and this affected only the M's, not the m's. The Leslie–DeLury method is used to obtain the initial estimate (Run 0). This initial estimate is used to compute the dispersion matrix Var(e) for the first iteration (Table 3). The estimates of the population size converge to within two fish by the first iteration and all the variables computed converge to within the number of digits reported by the second iteration. The population size estimate obtained using the corrected Leslie–DeLury method is $\hat{N}_1 = 11525$ with $\text{SE}(\hat{N}_1) = 493.1$ and the estimate obtained by generalized least squares is $\hat{N}_1 = 11407$ with $\text{SE}(\hat{N}_1) = 840.2$.

TABLE 2. Catch (number of sockeye salmon fingerlings) and effort (m^3 swept by a dip-net) data for the estimation of abundance in a hatchery pond.

	$i = 1$		$i = 2$		$i = 3$		$i = 4$		$i = 5$		$i = 6$	
j	C	f	C	f	C	f	C	f	C	f	C	f
1	181	1.96	90	1.44	53	1.00	42	0.75	33	0.90	46	1.62
2	202	2.24	11	0.16	59	0.75	100	2.00	100	3.00	23	0.81
3	84	0.84	14	0.16	65	1.00	98	2.25	88	2.70	16	0.54
4	118	1.12	94	1.60	93	1.50	13	0.25	89	2.70	8	0.54
5	87	1.12	69	0.96	112	1.75	53	1.25	21	0.60	26	0.81
6	157	1.68	32	0.64	121	2.25	40	0.50	58	1.50	29	1.08
7			109	1.44	80	1.50			15	0.60	64	2.70
8			85	1.12					70	2.10	4	0.27
9									79	2.10		
10									69	2.10		
M	19		20		23		20		19		20	

TABLE 3. Results from the conditional regressions of catch upon effort, results from the first two iterations of the generalized least squares regression, and the estimated dispersion matrix Var(e) from the second iteration.

i		1	2	3	4	5	6
m		6.0	8.0	7.0	6.0	10.0	8.0
M		18.8	20.6	22.8	19.9	19.3	20.4
$\hat{C}_i$		2600.0	1300.0	1900.0	1150.0	1200.0	550.0
CPÛE		92.5	67.0	59.8	49.4	34.0	25.8
Var ($\hat{C}$)		52 850.0	26 299.0	19 841.0	25 451.0	7107.0	6761.0
Var (CPÛE)		7.6	11.6	6.8	14.9	0.48	2.1
Cov (CPÛE, $\hat{C}$)		−19.2	68.7	−55.7	−283.0	−5.1	3.0
Run	$\hat{\beta}_0$	SE ($\hat{\beta}_0$)	$\hat{\beta}_1 = -\hat{q}$	$E(\hat{\beta}_1)$	Cov ($\hat{\beta}_0$, $\hat{\beta}_1$)	$\hat{N}_1$	SE ($\hat{N}_1$)
0	101.473	3.780	−0.008830	0.0006481	−0.002219	11 525	493.1
1	101.528	3.362	−0.0089410	0.0006067	−0.000131	11 405	835.3
2	101.518	3.367	−0.0089396	0.0006105	−0.000131	11 407	840.2

$$\text{Var}(e) = \begin{bmatrix} 8.82 & 1.49 & 2.60 & 4.64 & 2.15 & 2.08 \\ 1.49 & 15.73 & 5.77 & 7.80 & 5.32 & 5.24 \\ 2.60 & 5.77 & 14.02 & 9.64 & 7.16 & 7.09 \\ 4.64 & 7.80 & 9.64 & 25.84 & 8.97 & 8.90 \\ 2.15 & 5.32 & 7.16 & 8.97 & 10.61 & 10.20 \\ 2.08 & 5.24 & 7.09 & 8.90 & 10.20 & 12.72 \end{bmatrix}$$

Discussion

Equation (4) shows that the corrected Leslie–DeLury method has measurement errors in the independent variable when the total catch is estimated. These estimation errors make the corrected Leslie–DeLury model an errors-in-covariates structural model and estimates obtained by applying conditional regression to this type of model are known to be biased (Moran 1971; Seber 1977). Nevertheless, this bias can be avoided by using a controlled variables design.

A second difficulty with the corrected Leslie–DeLury approach is that the dispersion matrix is misspecified since $\text{Var}(e) \neq \sigma^2 I$: for example we estimate the dispersion matrix for the fingerling data and find that it has unequal diagonal elements and large off-diagonal elements (Table 3). However, despite misspecification of the dispersion matrix, when ordinary linear regression is applied, estimates remain unbiased on the average if the rest of the model is correctly specified, such as when the total catches are known or in the controlled variables design (Seber 1977; Draper and Smith 1981). For the fingerling data, the corrected Leslie–DeLury and generalized least squares estimates of the initial population size differ by only 118 fish out of approximately 11 500. That is a factor of only 1.0%.

However, the generalized least squares estimate is the minimum variance unbiased linear estimate (Seber 1977; Draper and Smith 1981) and, hence, although the corrected Leslie–DeLury estimate may be reliable, generalized least squares will give, on the average, more precise estimates from the same data.

Another important difference between the corrected Leslie–DeLury and generalized least squares methods is in their estimated variances. When the dispersion matrix is misspecified ordinary linear regression gives biased variance estimates but generalized least squares gives unbiased variance estimates (Seber 1977; Draper and Smith 1981). For the fingerling data the standard error of the population size estimate obtained by using the corrected Leslie–DeLury method is 41% smaller than is obtained by using the generalized least squares estimate. Since the generalized least squares estimate is minimum variance, this not only demonstrates that the variance estimate obtained by using the corrected Leslie–DeLury method is biased, but that this bias can be substantial.

The corrected Leslie–DeLury method has been employed in a wide range of uses. We hope that the generalized least squares

method will replace it and will be similarly useful. However, as with all statistical estimators, the generalized least squares method has predictable statistical properties only subject to the conditions defined by its underlying assumptions. Furthermore, it is less general than the corrected Leslie–DeLury method as it is restricted to applications where sample variances can be computed for the individual CPUE's and where a controlled variables design can be implemented. However, we feel that sample variances can usually be computed and the requirements of this design can often be attained especially when this requirement is known beforehand.

If the assumptions underlying our method are not met for some particular application, we would recommend considering the many alternative CPUE methods which have been developed for other sets of underlying assumptions. Reviews of some of these methods are presented by Gulland (1956, 1977), Rothchild (1977), and Mangel (1982). Some other methods are also presented by Butterworth (1979), Gavaris (1980), Collie and Sissenwine (1983), Mangel and Beder (1985), and by others.

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River Spawning of Artificially Reconditioned Atlantic Salmon (*Salmo salar*)

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We present information on the reproduction of artificially reconditioned Atlantic salmon (*Salmo salar*) in an enclosed spawning area and report evidence that some of these fish are fit for natural spawning 1 yr after their previous reproduction as wild fish, in spite of numerous treatments and manipulations.

Cette note présente certaines informations sur la reproduction, dans un enclos en rivière, de saumons (*Salmo salar*) reconditionnés artificiellement. On y démontre que ces saumons sont aptes à frayer naturellement 1 an seulement après s'être reproduits à l'état sauvage, en dépit des multiples traitements et manipulations qu'ils ont subis.

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Among stocks of Atlantic salmon (*Salmo salar*) in eastern Canada, spawner escapement in the last few years has remained beneath the numbers required for an optimal use of available river habitat (Chadwick 1985). In order to stop the downward trend, reconditioning of kelts for artificial spawning has been suggested as a way to produce more juveniles (Ducharme 1972). There is an increasing interest for kelt reconditioning among salmon stock managers. Literature reviews and workshop proceedings on this subject have been published in recent years (Lévesque and Magnan 1985; Lévesque et al. 1985; Walsh et al. 1985). Experiments by Johnston et al. (1987) provide new and useful knowledge on the effects of photoperiod, temperature, and diet on kelt physiology and reconditioning.

This note is about a field test of one possible use of mended kelts, releasing them into the rivers for spawning. This would provide an easier, less expensive method to improve recruitment than stocking with eggs or juveniles from those fish.

Materials and Methods

Fifteen salmon, nine males and six females, from Bonaventure River (Gaspé Peninsula, Québec) were used for this test. They were caught by net near spawning grounds in December 1984 or by cast-fishing in the lower part of the river in April 1985. They were tagged and then placed in 12 000-L tanks of fresh water where they were held for 6–10 mo (Gauthier 1985). All kelts were fed with smelt (*Osmerus mordax*) or capelin (*Mallotus villosus*) as soon as they accepted it. In order to induce their feeding, kelts captured in December were gradually shifted from a photoperiod of 10L:14D on January 31 to a spring photoperiod of 14L:10D on February 16 (Turgeon 1985). Whenever a wound was seen on a fish, all of them were treated with malachite green.

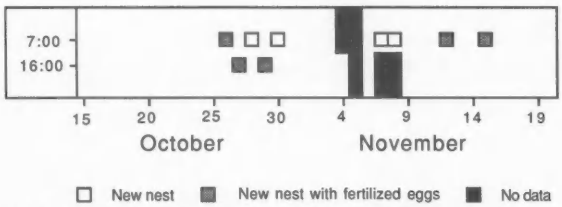

FIG. 1. Date and time when new nests were found in the enclosure. Missing data are due to an increase in water turbidity caused by repairs to a bridge, 500 m upstream.

An enclosure for this experiment was built before spawning time in Hall River, a tributary of Bonaventure, 9 km upriver from Chaleur Bay, in a stretch where wild fish have been seen spawning in previous years. The enclosure was about 90 m long, with its longer wall parallel to the shorelines and two shorter walls closing into the right shore. The enclosure walls were about 1 m high. They were made with 5-cm steel wire mesh attached to iron poles driven into the river bed. The wire mesh was buried 30 cm deep into the cobble to ensure that no salmon could pass under it. Within the 945 m^2 enclosed area, water velocity varied from 50 to 90 $cm \cdot s^{-1}$ and depth ranged from 15 to 80 cm.

Ten reconditioned salmon (seven males and three females) were placed in the enclosure on October 14, 1985, and five more (two males and three females) were added on October 25. Every salmon was sedated with MS-222, measured, weighed,

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TABLE 1. Data on reconditioned salmon held in the experimental enclosure. All salmon survived until the 1986 spawning season. The missing data are due to tag loss. Length and weight are when captured (A), before (B), and after (C) the experiment, and before (D) and after (E) the 1986 spawning. The apparent decrease in length for some fish during the experiment is probably an artefact due to flexions in the body of the live fish in the measuring box.

Tag number	Sex	Date captured	Date placed in enclosure	Length (mm)					Weight (kg)					Weight gain or loss (%)				Condition index				
				A	B	C	D	E	A	B	C	D	E	AB	BC	CD	DE	A	B	C	D	E
126001	M	84/12/12	85/10/14	540	640	630			1.00	2.00	2.00			100	0			0.64	0.76	0.80		
126008	M	84/12/12	85/10/14	550	680	680	730		1.25	3.25	3.00	3.75		160	−8	25		0.75	1.03	0.95	0.96	
126003	F	84/12/12	85/10/14	740	795	785	825	825	3.00	5.00	4.75	6.50	5.25	67	−5	37	−19	0.74	1.00	0.98	1.16	0.93
126007	F	84/12/12	85/10/14	740	770	760	820		3.25	4.00	3.25	5.75		23	−19	77		0.80	0.88	0.74	1.04	
1465	M	85/04/25	85/10/14	595	710	695			1.50	4.00	3.50			167	−13			0.71	1.12	1.04		
1481	M	85/04/25	85/10/14	770	875	860	940		3.25	6.50	5.75	8.50		100	−12	48		0.71	0.97	0.90	1.02	
1484	M	85/04/25	85/10/14	750	810	810			2.75	4.25	4.00			55	−6			0.65	0.80	0.75		
1500	M	85/04	85/10/14		710	700	710			4.25	4.00	5.00			−6	25			1.19	1.17	1.40	
1501	M	85/04	85/10/14		650	645	720			3.25	3.00	4.00			−8	33			1.18	1.12	1.07	
1499	F	85/04	85/10/14		700	705	760			3.25	3.00	4.75			−8	58			0.95	0.86	1.08	
126002	M	84/12/12	85/10/25	800	830	830	920		3.50	4.25	4.00	8.25		21	−6	106		0.68	0.74	0.70	1.06	
126005	F	84/12/14	85/10/25	725	790	780	840		2.75	5.75	4.25	7.00		109	−26	65		0.72	1.17	0.90	1.18	
126009	F	84/12/12	85/10/25	730	810	805	850		2.75	5.50	4.00	5.50		100	−27	38		0.71	1.03	0.77	0.90	
1503	M	85/04	85/10/25		805	805				5.00	4.75				−5				0.96	0.91		
1502	F	85/04	85/10/25		850	845				5.75	4.50				−22				0.94	0.75		

dipped into a malachite green solution and placed in the enclosure. Within 2 or 3 min, the effects of anaesthesia had vanished and the fish were swimming or holding position normally.

The enclosure was visited twice daily, at 7:00 and at 16:00, for the 38 d of the experiment. Notes were taken on interactions between individuals, on the position held by every fish, on any evidence of digging or nest construction, and on the presence of eggs in any new nest. The time spent for every visit depended on how much activity occurred. The mean observation time per visit was over 1 h. Night observation equipment was not available for this experiment.

All fish were removed from the enclosure on November 20. They were reconditioned once more in the following year. The presence of eggs or milt was checked in every fish at spawning time in 1986.

Results

Complete spawning acts of female 126 005 with male 1481, including egg covering by the female were observed twice (on October 26 and 27). Parts of other spawning sequences were also seen with different pairs involved (female 126 009 with male 1481; unidentified female and male). Although some spawning activity was seen during daytime, other data suggest that most spawning occurred at night, a time when no observation could be made. Among the nine newly-dug redds noted during visits to the site, seven were found in the morning and two in the afternoon (Fig. 1). Five more redds were not visible from the shore and were discovered upon wading into the river to dismantle the enclosure on November 20. Thus the total number of nests dug from October 14 to November 19 might well be over 14. Fertilized eggs were found in seven out of 14 nests. As the search for eggs did not go beyond removing a few cobbles, this number is also considered to be a minimum.

Three wild grilse entered the enclosure through the wire mesh on October 28 and had to be left inside because their capture would have disturbed the other salmon. All three were males, judging by the aggressive interactions that male 1481 consistently won over them. The wild grilse could have fertilized some eggs but not all of them; two nests with fertilized eggs were found before they entered the pen.

Five out of six females are believed to have spawned in the enclosure. This is based on comparisons of their weight before and after the experiment (Table 1) and on clear changes in their general appearance, such as extensive scale loss and flaccid flanks. Females with tag number 1499, 1502, 126 005, 126 007, and 126 009 lost 8–27% of their weight during the 38 d in the enclosure and this difference is attributed mostly to egg expulsion. Four of these females kept their tag until the next spawning season and did not produce ripe eggs in 1986. Female 1499 lost only 8% of her initial weight while in the enclosure but she showed other signs of spawning. She also had the smallest initial weight and her weight loss might be partially obscured by the crude methods for weighing live fish in the field. Female 126 003 most probably did not spawn in 1985. She lost only 5% of her weight, did not appear slimmer after the experiment and showed no extensive scale loss. This female was spawned artificially the following year (1986), losing 19% of her weight.

Data on males do not allow us to determine which ones reproduced, except for male 1481, which was seen spawning. Because of the mesh size of the enclosure walls, the contribution of precocious parrs to egg fertilization cannot be ruled out. However, previous artificial spawning experiments with reconditioned male and female salmon fed an adequate diet showed that their eggs and milt produced offspring with a survival to smolt stage similar to those from maiden fish (Ducharme and Gray 1985).

Discussion

The observed spawning, the nests found, some of them with fertilized eggs, and the weight loss of five out of six females are taken as evidence that some reconditioned salmon are fit to reproduce within 1 yr of their previous spawning as wild fish. The reintroduction of artificially reconditioned salmon in the river could be an interesting alternative to egg or smolt transplants, because of its lower costs. This use of mended kelts

might be more efficient that producing and transplanting eggs because the spawners would choose the best suitable spawning grounds. Another advantage would be that reconditioned salmon could be used to restore populations in some river parts otherwise inaccessible for egg transplants.

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Structural Organization and Species Composition of a Lotic Periphyton Community in Response to Experimental Acidification

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Changes in species composition, richness, diversity, biomass (biovolume), and spatial community structure of a lotic periphyton community were observed under experimental acidification (mean pH 4.5) with and without aluminum, in troughs fed from an oligo-dystrophic creek (mean pH 6.7). In experimental and control troughs, the community was dominated by diatoms throughout the treatment. *Achnanthes linearis* was dominant in all troughs before treatment as well as in the control during the experiment. *Eunotia pectinalis*, which was rare in all troughs before treatment, became dominant in the acidified troughs. After 3 mo of acidification, algal cell density and biomass were respectively 30 and 40–70 times higher in the treated troughs as compared with that in the control. The low diversity ($H = 1.45–2.30$) characteristic of the control trough, increased to 3.3 in the treated troughs after 1 mo of acidification, but after 3 mo of experiment the diversity was slightly lower in experimental troughs. In the control trough, spatial organization of the community was characterized by monolayered arrangements during the whole experiment. In both acidified troughs (acid and acid plus aluminum) the community became multilayered (3–4 layers). The increased complexity of the community in the acidified troughs seemed to be related to a decrease in the abundance of grazers in the periphytic community, mainly the collector–gatherers Ephemeroptera and Orthocladiinae.

On a observé des modifications de la composition en espèces, de la richesse, de la diversité, de la biomasse (biovolume), et de la structure spatiale des populations d'un périphyton lotique soumis à une acidification expérimentale (pH moyen de 4,5), avec et sans aluminium, dans des bassins alimentés par un ruisseau oligotrophe (pH moyen de 6,7). Dans les bassins expérimentaux et témoins, les diatomées ont prédominé pendant toute la durée du traitement. *Achnanthes linearis* a dominé dans tous les bassins avant le traitement ainsi que chez les témoins au cours de l'expérience. *Eunotia pectinalis*, rare dans tous les bassins avant le traitement, est devenue dominante dans les bassins acidifiés. Après 3 mo d'acidification, la densité des algues et la biomasse étaient respectivement 30 et 40 à 70 fois plus élevées dans les bassins traités que dans les bassins témoins. La faible diversité ($H = 1,45–2,30$) du bassin de contrôle a augmenté à 3,3 dans les bassins traités après 1 mo d'acidification, mais au bout de 3 mo d'expérience, la diversité était légèrement plus faible dans les bassins expérimentaux. Dans le bassin témoin, les populations se sont réparties en monocouches pendant toute la durée de l'expérience. Dans les deux bassins acidifiés (acide et acide plus aluminium), les populations se sont réparties en plusieurs couches (3 à 4 couches). La complexité accrue des populations dans les bassins acidifiés semblait être reliée à une diminution de l'abondance des brouteurs dans le périphyton, principalement les éphéméroptères et les orthocladiinés, qui sont des collecteurs–cueilleurs.

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Lotic periphyton communities usually respond to environmental acidification by increasing either their biomass alone (Hendrey 1982; Muller 1980; Mulholland et al. 1986), or both their biomass and productivity (Hendrey 1976; Parent et al. 1986). To our knowledge a decline of periphyton biomass was reported only once in relation to acidification (Stokes 1984).

Several hypotheses have been put forward to explain the increase in periphyton biomass: (1) an increase in available nutrients either by resolubilization from the sediments, or by nitrogen and sulfur additions from the acidifying agents (NO_x and SO_x); (2) a reduction in grazing by micro and macrobenthic organisms because of the disappearance of certain species sensitive to acidification; and (3) a change in algal species composition with a dominance of species better adapted to habitats with high concentrations of hydrogen ions or metals. There various hypotheses are not mutually exclusive, and the proposed mechanisms can operate simultaneously.

Although the first hypothesis has already been demonstrated (Planas and Moreau 1986), the other two cannot be definitively excluded or confirmed. The role of grazing has been stated but not thoroughly analysed (see reviews by Hendrey 1982; Stokes 1986).

Species composition of the periphytic community of acidified habitats has been studied mainly in lakes (Hendrey and Vertucci 1980; Lazarek 1982; Schindler et al. 1985; Turner et al. 1986). For lotic waters however, there is much less information and that which is available deals mostly with acid mine

drainage (Whitton 1972; Lampkin and Sommerfield 1982; Deinseger et al. 1986). In a study of various rivers of different pH (Mulholland et al. 1986) it appeared that the communities of acidified streams are dominated by Chrysophyceae as well as diatoms of the genus *Eunotia*, which replace the cyanophytes abundant in habitats approaching neutrality.

The objectives of this study were

(1) to verify if a change in species composition occurs as a result of a pH decrease in lotic systems,

(2) to determine the role of invertebrate grazing through the study of periphytic community microstructure.

The changes in species composition and biomass of the periphyton community were established by cell counts and biovolume determinations.

The analysis of changes in the periphyton community microstructure was done by scanning electron microscopy. The structure of the periphyton community can be modified by environmental instability, as well as by grazing. Without disturbance, succession causes structural complexity to develop (Hudon and Bourget 1983; Hoagland et al. 1982; Korte and Blinn 1983; Hamilton and Duthie 1984). In disturbed environments, however, periphyton communities never attain such states of organization and thus remain at the early stages of colonization (McIntire 1966; Hudon and Bourget 1983; Luttenton et al. 1986).

For our study, the experimental design used previously (Serodes et al. 1984; Parent et al. 1986; Allard and Moreau 1987a, b) is particularly suitable because it eliminates interference from certain external physical factors (nature of the substrate, current velocity, and light) which can influence the species composition and structural complexity of the community (Tett et al. 1978; Horner and Welch 1981; Stevensen 1983; Millie and Low 1983).

Since the high aluminum concentrations accompanying acidification usually have a toxic effect on organisms in natural environments, our experimental set up comprised two sets of conditions: (1) acidification only and (2) acidification with the addition of aluminum.

Materials and Methods

The experiments were set up at the Laval University research station in Montmorency Forest, located 100 km north of Québec City (47°19′N, 71°07′W) in a boreal forest. This region is characterized by abundant total precipitation (the annual mean for the last 15 yr is 1500 mm) a mean rainfall pH of 4.3 and average concentrations of sulfate and nitrogen oxides of 41.1 and 26.8 $\mu eq \cdot L^{-1}$, respectively (Papineau 1987).

The troughs used for the experiments were described in detail elsewhere (Serodes et al. 1984). Briefly, the experimental set up consisted of uncovered plasticized wooden troughs, 6 m long and 20 × 20 cm in cross section. Water depth in the troughs was maintained at 18 cm, with a reservoir at the head from which water flowed continuously by gravity at a constant rate of 3 $L \cdot s^{-1}$ (flow velocity approximately 0.2 $m \cdot s^{-1}$).

The streamwater diverted into the system was of the oligotrophic–dystrophic type with a pH varying from 6.1 to 7.1. Details of water physico-chemistry can be found in Parent et al. (1986).

The artificial substrates used for periphyton colonization consisted of unglazed ceramic tiles, each having an area of 10 cm^2. In order to maintain the same orientation for all tiles, they were placed on transparent plastic supports at an angle of 45° from the bottom. The bottom of the troughs was covered with calibrated granite pebbles (2–4 cm diameter). Tiles were placed in the troughs 4–6 wk before treatment to be colonized by organisms drifting into the troughs. Previous experimentation had shown that 3 wk was sufficient time to obtain a periphytic biomass representative of the creek.

Sulfuric acid (3.5 N) added using a peristaltic pump decreased the pH of the experimental trough from a mean of 6.5 to within the range of 4–4.6. In one of the troughs aluminum sulfate was added to obtain a mean concentration of 400 $\mu g \cdot L^{-1}$ (230–520 $\mu g \cdot L^{-1}$) in the water (80% in monomeric form, 50%

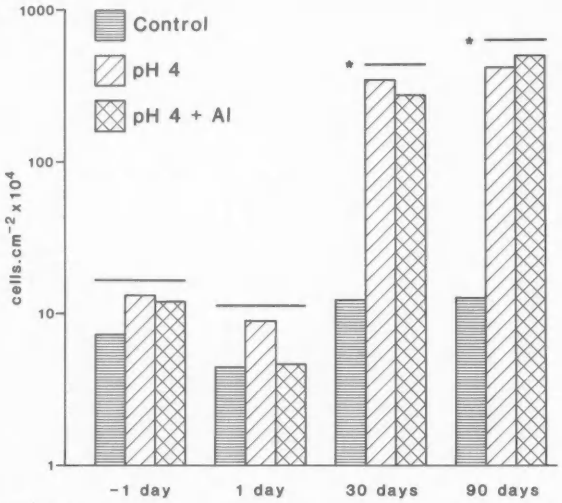

FIG. 1. Temporal changes in periphyton cell density in the control, acidified, and acidified plus aluminum troughs. X axis: time scale; before (−1) and 1, 30, and 90 d after acidification. Y axis is in logarithmic scale. Lines above the histograms represent nonsignificant differences between treatments and the asterisk indicates those that were significantly different.

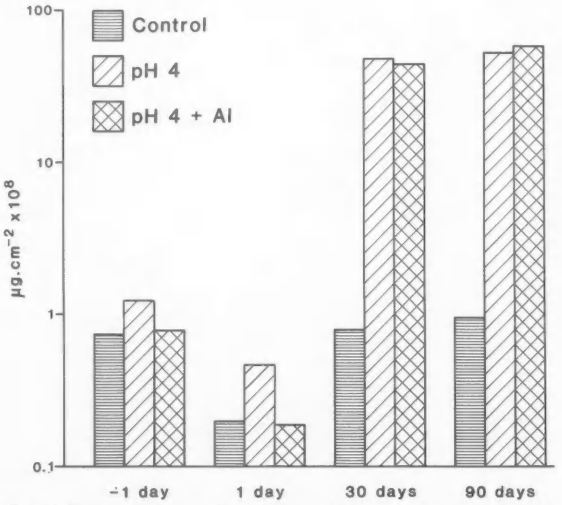

FIG. 2. Temporal changes in periphyton biomass in the control, acidified, and acidified plus aluminum troughs. See legend of Fig. 1 for the description of the axes.

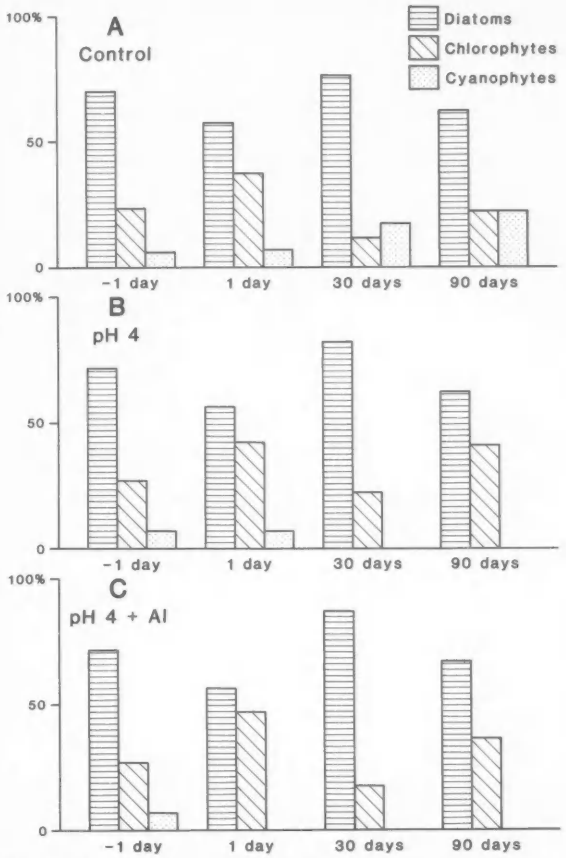

FIG. 3. Temporal changes in cell density (percent) of the dominant groups of algae. See legend of Fig. 1 for the description of the X axis. (Densities inferior to 1% are not represented).

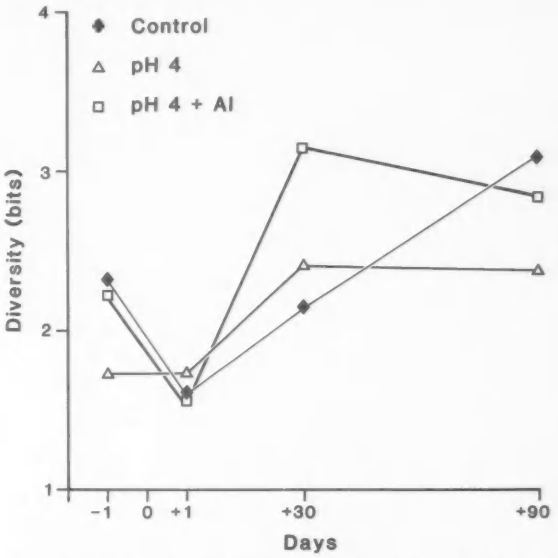

FIG. 4. Temporal changes in species diversity. See legend of Fig. 1 for the description of the X axis.

in inorganic form) in addition to the sulfuric acid. This range of pH and aluminum concentrations has been observed in many lake inflows of the Laurentide reserve, especially during spring and fall (Moreau et al. 1984; and D. Planas, unpubl. data). One trough served as a control.

Sampling was carried out every 3 wk with simultaneous measurement of water chemistry, periphyton metabolic characteristics (Parent et al. 1986), macrobenthos community composition (Allard and Moreau 1987a,b), and benthic metabolism (Allard and Moreau 1985).

For cell counts, two tiles (10 cm^2 each) were randomly removed from each trough and immediately immersed in 100 ml of distilled water. The growth was brushed off carefully, fixed with Lugol's solution and counted using an inverted microscope at 600× (Utermöhl 1958). The number of fields counted was determined using the Venrick (1978) procedure. Acid-cleaned subsamples were used for diatom identification. The biomass was estimated by cell volume. The biovolume for each species was calculated using the mean dimension of 10–20 specimens for the more abundant species, or literature data for the rare species.

Prior to experimentation, each tile to be examined by scanning electron microscopy (SEM) was divided into two parts. These tiles were held together on a support to maintain the geometry of the system. Immediately after sampling, they were frozen in liquid nitrogen, transported to the laboratory and freeze-dried for 12 h. Eventually they were mounted on a stub with silver and coated with gold-palladium.

Diversity indices were calculated on cell counts using Shannon's equation (Legendre and Legendre 1983) and statistical comparisons were carried out using the Kruskal–Wallis test followed by nonparametric multiple comparisons.

Results

Community Composition

Periphyton density (Fig. 1) and biomass did not vary significantly between troughs before and 1 d after the beginning of acidification (Fig. 2). After 1 and 3 mo of acidification, no significant difference in abundance (number or biomass) was observed between the two acidified troughs (acid and acid plus Al), however the abundances in these two troughs were significantly different from those in the control trough. After 3 mo of treatment the density and the biomass were, respectively 30 and 40–70 times higher in the acidified channels than in the control trough.

Initially the community was dominated by diatoms as is common for a first order stream (Patrick 1977) (Fig. 3). This dominance continued throughout the experiment. Chlorophytes ranked second in importance prior to acidification but at the end of the experiment had declined in the control channel, while remaining stable under the experimental conditions.

The cyanophytes, initially representing less than 7% of the population, increased with time in the control trough (to 19.4%) but were greatly reduced in the experimental troughs (after 1 d of experiment: 3.2% with acid alone, 1% with acid and aluminum; after 90 d of treatment: 0.8% with acid alone, 0.9% with acid and aluminum).

Under all three conditions, the species richness of these communities was high, with an average of 41 species identified per sample. This is comparable with that observed by Hamilton

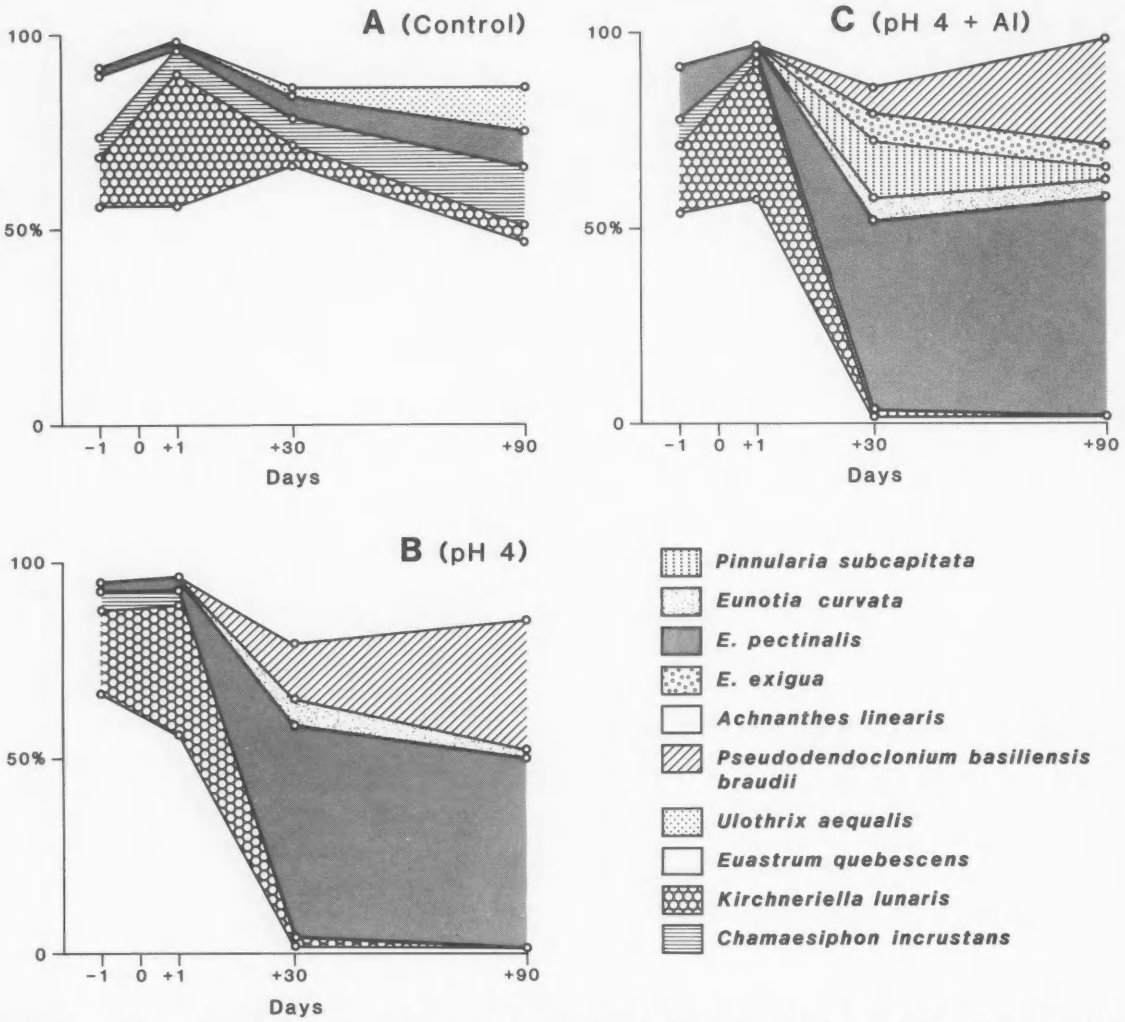

FIG. 5. Temporal changes in species abundance (species representing more than 5% of the total sample). See legend of Fig. 1 for the description of the X axis.

and Duthie (1984) in periphyton samples from Canadian Shield streams. In spite of this richness, diversity (*H*) was relatively low, varying between 1.45 and 2.30 (Fig. 4), due to the dominance of a few (three to four) species (evenness between 0.52 and 0.73). After 1 mo of treatment, diversity was higher in the experimental troughs than in the control, but after 3 mo of experiment the diversity was slightly lower in experimental troughs (Fig. 4). These results are not in agreement with those of several authors (see review by Hendrey 1982) suggesting a decrease in species richness. As mentioned in Stokes (1986) diversity seems a poor measure of the effect of acidification on periphyton communities.

The relative abundances of the various species differed considerably between the control and the acidified troughs (Fig. 5). In the control, community composition was characterized by the constant dominance of *Achnanthes linearis* (W. Sm.) Grunow (45–65% of the total community). In the acidified troughs however, this species became relatively rare, accounting for less than 3% after 1 mo of treatment. At this period, the dominant species (50%) was *Eunotia pectinalis* (Kütz.) Rabh. This species is considered acidophilic (Steinman and Sheath 1984) and typical of cold, poorly mineralized (Patrick 1977), well-oxygenated waters (Podzorski 1984). *E. pectinalis* was present but very rare in all three troughs before treatment began and remained rare throughout the experiment in the control trough.

The increase in chlorophytes in both acidifying treatments was due to the appearance and increased density of the colonial species *Pseudendoclonium basiliense brandii* Visher (Fig. 5).

The increase in relative abundance of cyanophytes in the control was due to the development of *Chamaesiphon incrustans* Grunow, an epiphytic species (Tilden 1968) attached to *Achnanthes* and *Ulothrix* (Fig. 5) in our experimental troughs.

Spatial Organization of the Community

After 1 mo of colonization, all three troughs supported communities with the same type of structural organization. The

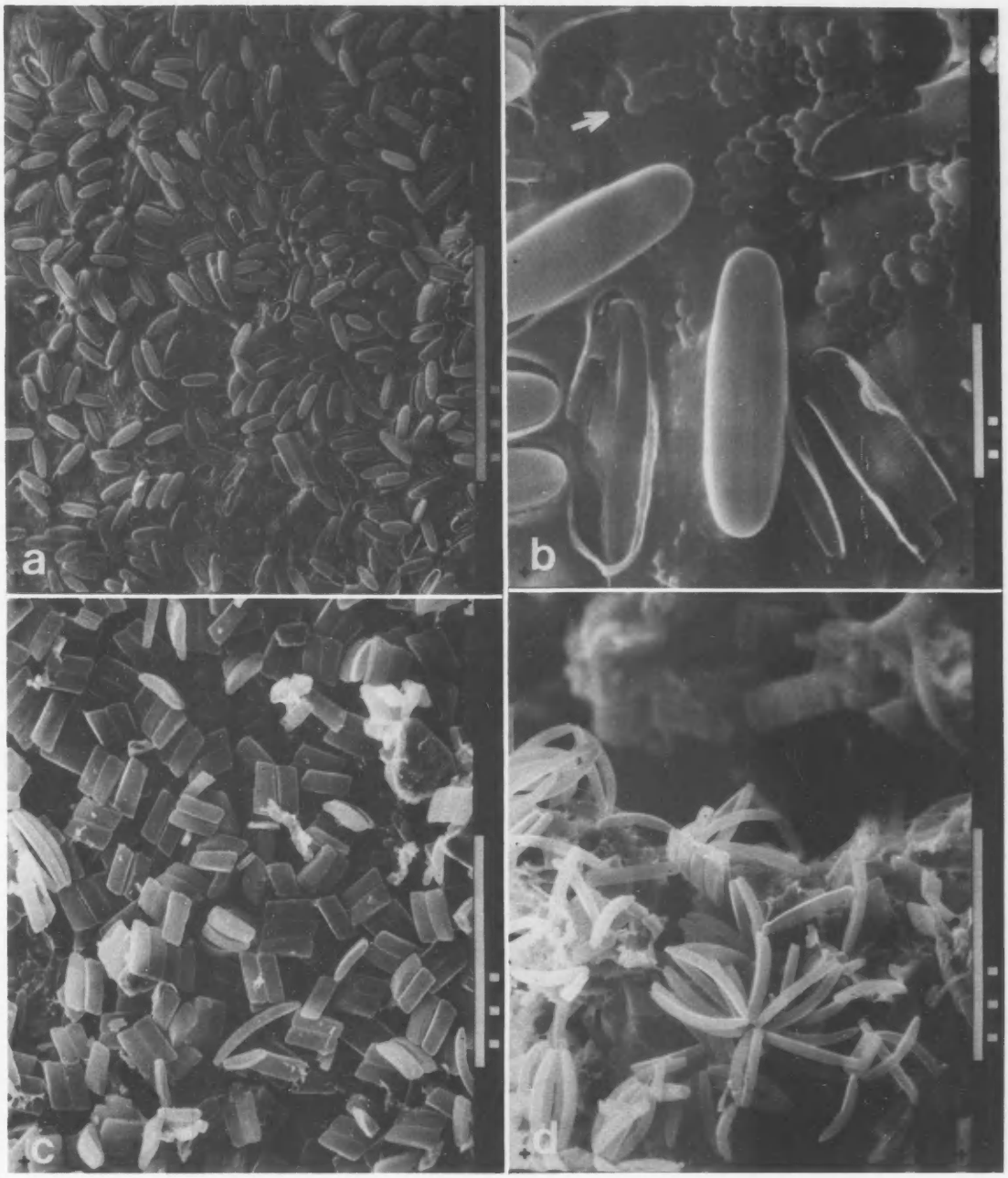

FIG. 6. Community structure viewed by scanning electron microscopy (a) monolayered growth of *Achnanthes linearis* in the control at the beginning of the experiment; scale = 100 μm. (b) bacteria-like forms (arrow) growing associated with *A. linearis* layer; scale = 10 μm, (c) multilayered growth of *Eunotia pectinalis* in the acidified trough after 1 mo of treatment; scale = 100 μm, (d) *E. curvata* growing on *E. pectinalis* in the acidified trough; scale = 100 μm, (e) multilayered growth of *E. pectinalis*, *E. curvata* and *Ulothrix* (arrow) in the acidified plus aluminum trough after 1 mo of treatment; scale 100 μm, (f) *Tabellaria floculosa* strain IV Koppen, *Pinnularis subcapitata*, and *Frustulia rhomboides var saxonica* in the acidified plus aluminum trough after 1 mo of treatment; scale = 100 μm, (g) control trough after 3 mo of treatment; scale = 10 μm.

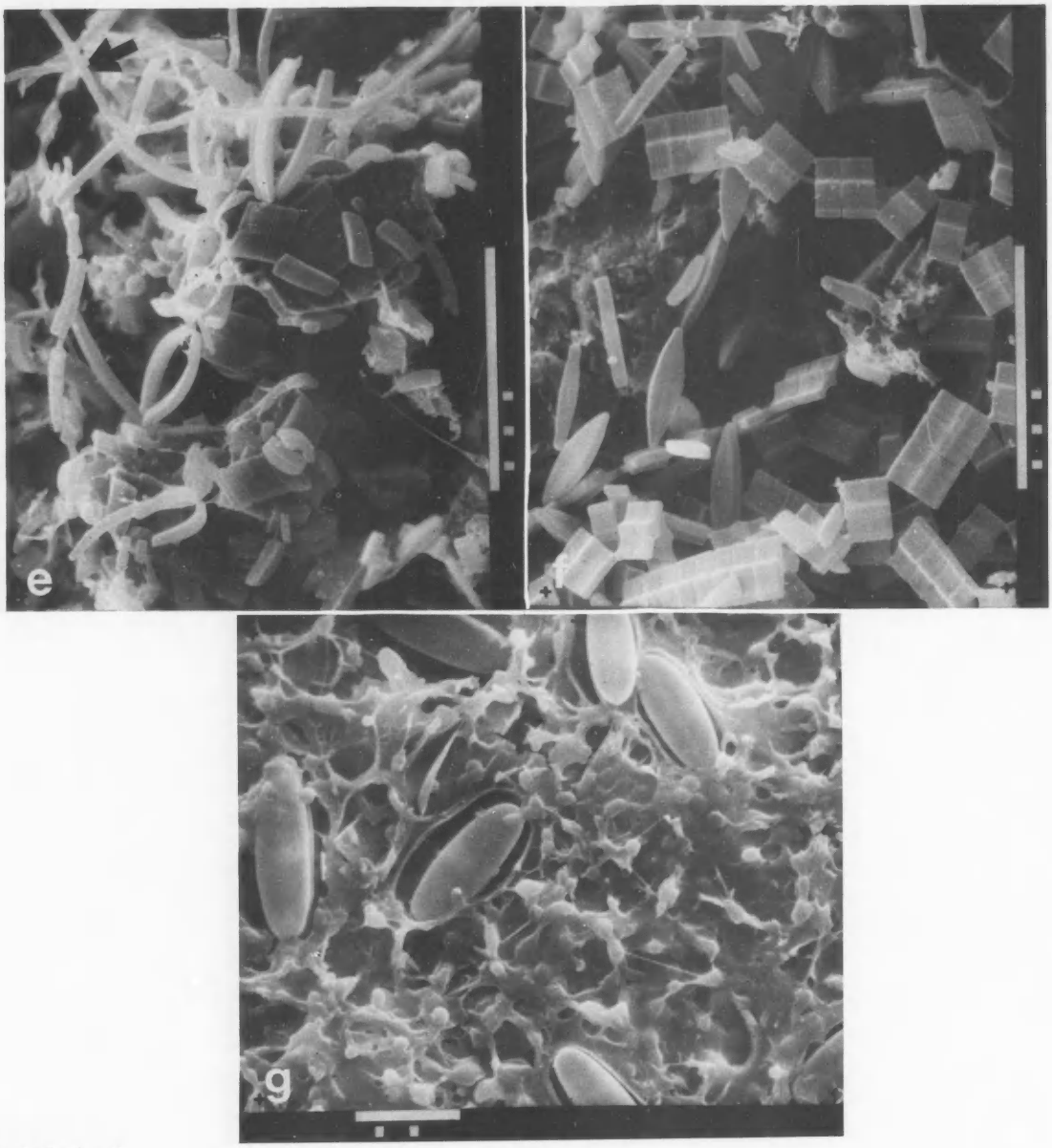

FIG. 6. *Continued*

communities were essentially characterized by a single layer of the dominant species *Achnanthes linearis* alternating with a multitude of small spheres (0.5–1.5 μm) similar to bacteria (Fig. 6a, 6b, and 7). The solitary nonmotile cells of *A. linearis* were surrounded by a uniform layer of mucilage similar to that reported for another species of the genus, *A. lanceolata* (Patrick 1977) and for other solitary prostrate benthic diatoms which characterize initial stages of colonization (Patrick 1977; Hoagland et al. 1982). This monolayer was covered here and there by a few rare specimens of other species such as *Eunotia pectinalis* (Fig. 6a). In the control trough this simple structure persisted throughout the experiment (Fig. 6g). The only notable changes observed were an increase of the mucilaginous envelope and an increase in the abundance of bacteria.

Under acidified conditions, both with or without aluminum, the structural organization had changed completely after 1 mo of treatment. At that point numerous layers of cells were apparent (Fig. 6c, 7). In the trough receiving only acid, three cellular strata could be distinguished. The basal layer was comparable to that of the control, composed of bacteria and *A. linearis*, although the latter was much less abundant than in the control. Overlying this, was a multilayered growth of *Eunotia pectinalis*, the dominant species at that period. This colonial diatom formed a loose structure of long ribbons parallel to the sub-

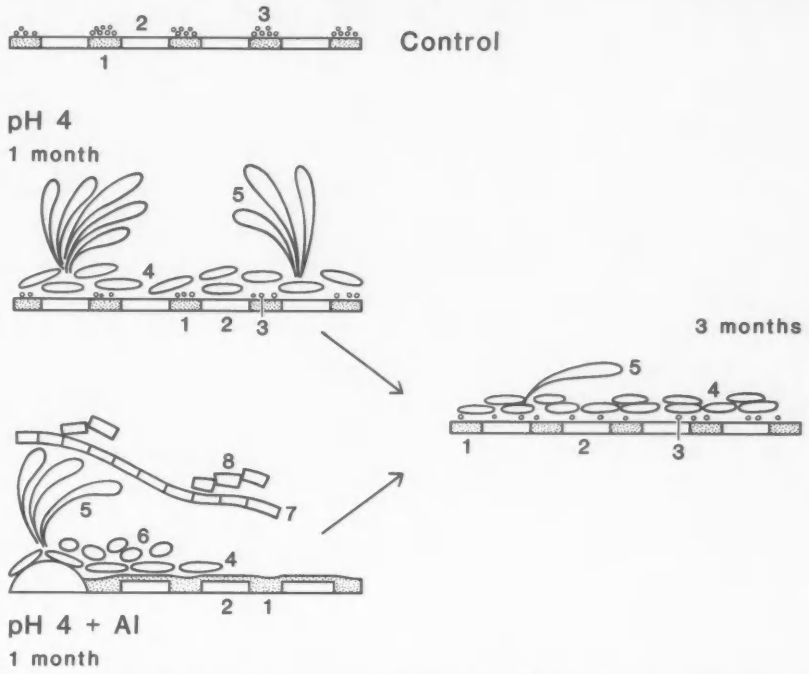

FIG. 7. Diagrams of the changes in community structure before and after 1 and 3 mo in the treated troughs (acidified, acidified plus aluminum); 1: Mucilage, 2: *Achnanthes linearis*, 3: bacteria, 4: *Eunotia pectinalis*, 5: *E. curvata*, 6: *E. exigua*, 7: *Ulothrix*, 8: *Tabellaria flocculosa*.

TABLE 1. Mean density (±1 SE) of total benthic invertebrates ($\times 10^2 \cdot m^{-2}$), main Chironomidae groups and Ephemeroptera families in the control (C) acid (A) and acid + aluminum (AA) troughs, 3 mo after acidification (data from Allard and Moreau 1987b).

	C	A	AA
Total density*	1700.6±79.2	632.6±34.9	671.0±57.4
Chironomidae			
Tanypodinae*	35.6±7.2	9.2±0.8	11.6±2.8
Orthocladiinae*	582.4±56.6	154.8±13.6	160.8±22.2
Tanytarsini*	64.8±4.6	24.4±4.6	30.8±3.8
Chironomini**	118.4±14.2	54.4±11.2	69.2±17.0
Ephemeroptera			
Baetidae*	12.0±3.6	0.4±0.4	0.0±0.0
Leptophlebiidae*	42.4±11.7	5.6±2.1	2.0±0.6
Ephemerellidae*	133.6±22.4	23.2±2.1	30.8±5.4

*$p \leq 0.01$.
**$p \leq 0.05$ Kruskal–Wallis followed by nonparametric multiple comparisons.

TABLE 2. Mean abundance ($\times 10^2 \cdot m^{-2}$) ±1 SD of acid sensitive Orthocladiinae genera in the control (C), acid (A) and acid + aluminum (AA) channels after 3 mo of acidification (data from Allard and Moreau 1987b).

	C	A	AA
Orthocladiinae			
Corynoneura*	40.0±11.7	1.6±0.4	0.4±0.4
Cricotopus*	23.6±2.1	3.2±1.8	8.4±2.6
Nanocladius*	29.2±9.9	0.8±0.8	1.6±0.8
Parametriocnemus*	83.6±2.5	8.0±1.4	3.6±1.2
Rheocricotopus*	343.6±37.5	133.6±10.9	133.6±17.8
Thienemanniella*	32.4±10.6	2.0±1.1	7.6±1.5

*$p \leq 0.01$ Kruskal–Wallis followed by nonparametric multiple comparisons.

stratum, which imprisoned other species of solitary diatoms. A third superficial stratum consisted of *E. curvata* fan-shaped colonies (Fig. 6d, 7). In the trough receiving acid and aluminum, the spatial structure was even more complex after a month of treatment. On top of the three layers previously described was a fourth composed of filaments of *Ulothrix aequalis* Kuetzing (Fig. 6e, 7) and chains of *Tabellaria* perpendicular to *E. curvata* and other solitary species of diatoms with a raphe (Fig. 6f, 7). In this experimental trough, the basal stratum was characterized by a thicker mucilaginous layer of *A. linearis* and an apparent decrease in bacteria. During the experiment the filamentous green algae *U. aequalis* declined in absolute abundance in the control, but increased in the treated troughs although its relative abundance never exceeded 5%.

At the end of the 3-mo experiment, the structures observed in both acidified troughs had changed slightly from those described above. Changes included a reduction in thickness and compactness of the *E. pectinalis* layer, a decrease in abundance of *E. curvata* and a disappearance of *Tabellaria* and *Ulothrix* in the trough with aluminum.

Discussion

The impressive increase in density and biomass of periphytic populations in the troughs that were acidified (with or without

aluminum) is comparable with that observed for chlorophyll-*a* (Parent et al. 1986). These modifications were accompanied by changes in species composition, with an increase in diatoms and, to a lesser degree, in cholorophytes. These results differ from the frequently observed increase in Zygnematales, described by Hendrey and Vertucci (1980); Stokes (1984); Schindler et al. (1985); or in cyanophytes (Lazarek 1982).

The change in relative abundance of the various species can be interpreted in two ways. First, the disappearance of certain species could be accompanied by the appearance of others according to differential sensitivity to H^+ ion concentration. Second, variations in relative abundance could be due to interspecific competition, as a result of trophic web modifications.

The considerable reduction in relative abundance of *Achnantes linearis* after 1 mo of acidification could be due to competition with *Eunotia pectinalis* and *Pseudendoclonium basiliense*. *A. linearis* is a pioneer prostrate species so it would probably be at a disadvantage as a result of the growth of other species forming multilayers, possibly through competition for light and nutrients. Given that *A. linearis* is reported to be an alkalophile by Podzorski (1984) and Charles (1985), although Patrick and Reimer (1966) classify this species as indifferent to pH, there could also be a direct toxic effect by the high H^+ ion concentration. The predominance of *E. pectinalis* under acidified conditions reflects a clear acidophilic preference (Patrick 1977; Steinman and Sheath 1984) and/or a reduction in grazing.

In contrast to what has been described for various other types of communities (phytoplankton, zooplankton, fish; see review by Haines 1981), the diversity of periphyton populations is not severely modified by acidification. The changes in the community are thus better described by changes in dominant species than by reduction in richness.

Grazing could potentially explain why the microstructure of the control community did not vary throughout the experiment. The two-dimensional microstructure observed in the control community usually corresponds to the pioneer stages of colonization described by numerous authors for marine and freshwater habitats (Hoagland et al. 1982; Korte and Blinn 1983; Lamberti and Resh 1983; Roemer et al. 1984). Similar results were obtained by Summer and McIntire (1982) who reported a change in periphyton composition due to grazing of easily accessible species, with the community being reduced to species typically adhering to the substrate and covered with mucilage like *Cocconeis placentula*. In the present experiment *A. linearis* had the same role as *C. placentula*, whereas *Eunotia*, *Tabellaria* and *Ulothrix* adhering poorly to the substratum were easily accessible to grazers. In our study, the absence of development of a tridimensional organization in the control troughs cannot be attributed to the effect of current (Tett et al. 1978), waves (Luttenton et al. 1986), or physical disturbances in general (Kauffman 1982), because these physical parameters were identical for all troughs. In the acidic troughs we observed a gradual change from a bidimensional to a tridimensional structure.

In our system, acidification reduced the macrobenthic community to almost one third of that in the control, the Orthocladiinae and Ephemeroptera being the most sensitive to acidification. (Table 1; Allard and Moreau 1987a,b). These collector–gatherers preferentially exploit poorly attached periphyton species and thus contribute to maintaining low algal biomass (Hunter 1980; Kessler 1981; Lamberti and Resh 1983; Cattaneo 1983).

According to Coffman et al. (1971) three of the six genera of Orthocladiinae that decrease in number after treatment (Table 2) are herbivorous and get 70% of their energy from algae. A fourth genus, *Cricotopus*, is a shredder of higher plant tissue (Lamberti and Moore 1984). In our troughs, higher plants were absent so we may assume that this genus exploits the periphyton as well. The Ephemeroptera, which are gatherers and collector–gatherers (Cummins and Klugg 1979), eating bacteria, detritus and algae (Lamberti and Moore 1984), almost completely disappear under acidified conditions (Table 1). The observed modifications in benthic fauna are thus completely consistent with a reduction in grazing pressure in the acidified troughs.

Decline in grazing is expected to result in an accumulation of periphyton biomass, according to the model proposed by Lamberti and Moore (1984). However, contrary to what Lamberti and Moore (1984) observed, our study showed this biomass to remain active (Parent et al. 1986), most probably because of a greater availability of phosphorus (range of SRP in acidic conditions was between <0.03 to 0.24 μM and <0.03 to 0.1 μM in the control, see also Planas and Moreau 1986). This greater availability of phosphorus and reduced grazing ultimately result in a modification of the structural integrity of the community, since the potential biomass and production within a monocellular layer organization is inevitably limited; the development of a multilayered arborescent structure facilitates optimal use of available light.

On the whole, our results support the idea that the three potential mechanisms that may be responsible for the increase of periphyton biomass and production could probably operate concurrently. The decrease of grazing pressure in the treated troughs could be the cause of the multilayer growth of algae, but the increase in phosphorus in the acidified milieu could also favour this growth. The presence of potentially toxic forms of aluminum in one acidic treatment apparently did not have any influence on the abundance of the dominant species of algae present at low pH, but increased hydrogen concentration may have directly or indirectly favoured (through reduction of grazing) the growth of *Eunotia*.

Acknowledgments

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Distinction between American Eels (*Anguilla rostrata*) of Different Geographic Origins on the Basis of Their Organochlorine Contaminant Levels

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This study presents evidence that organochlorine contaminant levels of fish tissues represent a valuable tool for stock discrimination. Variability of concentrations of 15 organochlorine contaminants allowed a discrimination among American eels (*Anguilla rostrata*) of unknown (captured during the migration down the St. Lawrence River) or known geographic origins. The study also exemplifies that information regarding environmental distribution of contaminants can be gained by comparing organic contaminant levels among groups of fish. Indeed we can infer from this study that mirex contaminated sediments have extensively (at least 400 km) drifted downstream from Lake Ontario in less than 19 yr.

Cette étude révèle que les niveaux de contaminants organochlorés des tissus de poissons constituent un outil valable pour la discrimination des stocks. La variabilité des concentrations de 15 contaminants organochlorés a permi une discrimination entre des anguilles d'Amérique (*Anguilla rostrata*) dont certaines avaient une origine géographique inconnue (capturées durant la dévalaison du fleuve Saint-Laurent) et d'autres une origine géographique connue. De plus, nous démontrons qu'une comparaison des niveaux de contaminants entre des groupes de poissons peut s'avérer une source valable d'information sur la distribution des contaminants dans l'environnement. Ainsi, cette étude nous permet de déduire que les sédiments contaminés par le mirex, en provenance du Lac Ontario, ont été transportés très loin (au moins 400 km) en aval en moins de 19 an.

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Methods of stock discrimination in fishes have been reviewed by Ihssen et al. (1981). Some of these methods are based on the chemical composition of tissues, which reflects both natural and anthropogenic characteristics of the environment. Moreau and Barbeau (1982), using heavy metal concentrations of muscles, were able to distinguish to some degree American eels (*Anguilla rostrata*) of known geographic origins. Recently, Dutil et al. (1985) have presented a new method of stock discrimination based on an organic contaminant. Using a criterion of presence/absence of mirex (a pesticide), they were able to estimate the contribution of Lake Ontario eels to the St. Lawrence River fishery in 1982 as 74% of the total catch. They concluded that organic contaminants appear to represent a better tool for stock discrimination than heavy metals, provided that they persist in the environment and are passed on to fish through the food chain. Indeed, contrary to heavy metals, organochlorine contaminants do not occur naturally in the environment and thus have a more heterogeneous distribution than heavy metals.

Environmental contamination by mirex occurred in a limited area and started between 1963 and 1968 (Holdrinet et al. 1978). In 1968, mirex was restricted to Lake Ontario and two of its tributaries, and was absent from the St. Lawrence River sediments (Holdrinet et al. 1978). Sediments have been identified as the major environmental compartment containing mirex (Strachan and Edwards 1983); mirex is virtually insoluble in water (Alley 1973) and there is no indication of atmospheric transport of this pollutant (Strachan et al. 1980).

Mirex has been detected in three out of 20 immature eels from Lake Saint-Pierre (Desjardins et al. 1983; Dutil et al. 1985), an 11 km wide enlargement of the St. Lawrence River located about 400 km downstream from Lake Ontario (Fig. 1). Based on current knowledge of mirex distribution, this was dismissed as evidence for presence of mirex in Lake Saint-Pierre, but was thought to represent unusual cases of extensive downstream movements of immature eels originating from Lake Ontario.

This study presents a new method of stock discrimination in fishes. Multivariate analyses of concentrations of 15 organochlorine contaminants (14 pesticides and PCB) in eels are used to distinguish their geographic origins. Furthermore, an application of this method, in conjunction with the detection of mirex in American eels and Lake sturgeons (*Acipenser fulvescens*) from Lake Saint-Pierre provides strong evidence that mirex was

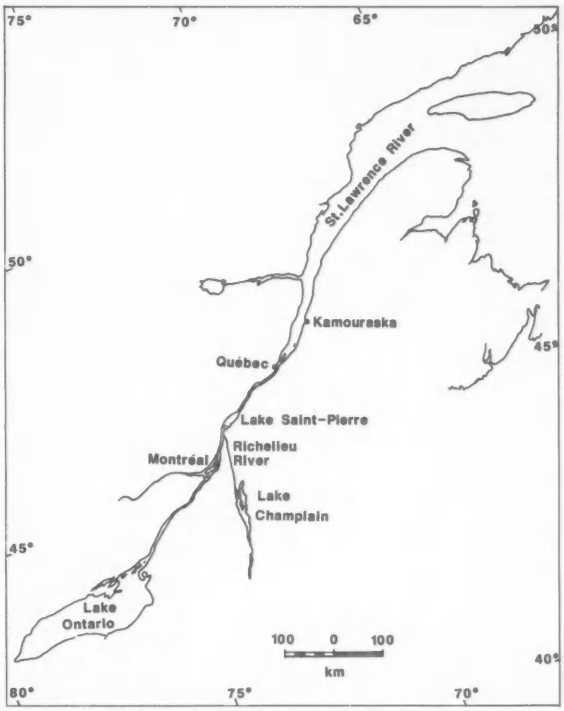

FIG. 1. Location of the sampling sites (Kamouraska, Québec, Lake Saint-Pierre, and Richelieu River).

TABLE 1. Location of capture (LSP: Lake Saint-Pierre), maturity stage (I = immature, M = maturing), mean total length, sample size (*n*), and percentage of eels in which mirex was detected.

Group	Location	Maturity	Mean length (mm)	*n*	Percent with mirex
KAM	Kamouraska	M	878	104	88
QUE	Québec	M	813	128	69
SPN	LSP-north[a]	M	861	59	88
SPS	LSP-south[a]	M	816	43	51
SPI	LSP	I	666	25	12
RIC	Richelieu	M	845	40	3[b]

[a]The separation between LSP-north and LSP-south was the navigation channel.

[b]Mixing of samples in the laboratory probably accounts for the presence of mirex in one eel from Richelieu River.

transported downstream from its source between 1963–68 and 1982, and is no longer restricted to Lake Ontario and its tributaries. In this study "stock" refers to a production or management unit as defined by Larkin (1972), but the method would be equally valuable for genetic stocks as defined by MacLean and Evans (1981). The term "geographic origin" refers to the freshwater area of residence of the eels during the immature stage.

Materials and Methods

Sampling

Contaminant concentrations were compared among six groups of eels distributed over five sampling sites along the St. Lawrence River and two maturity stages (Table 1, Fig. 1). The range of sampling dates were 8 June to 21 July 1982 for Richelieu River eels (RIC), 5 May to 28 July 1982 for Lake Saint-Pierre north eels (SPN), 1 May to 21 July 1982 for Lake Saint-Pierre south eels (SPS), 5 May to 21 July 1982 for immature eels from Lake Saint-Pierre (SPI), 23 August to 5 October 1982 for Québec eels (QUE), and 5 October 1982 (only one sample) for Kamouraska eels (KAM). Most (80%) SPI eels were caught on the southern side of Lake Saint-Pierre.

Maturing and immature eels were considered migratory and sedentary, respectively. Sexual maturity was determined from the oocyte diameters and the presence or absence of lipid droplets in the cytoplasm of the oocytes (Dutil et al. 1985). It was assumed that immature eels were captured where they had spent the sedentary part of their life cycle. Except for RIC eels, the geographic origin of the maturing eels within the St. Lawrence watershed was unknown, as they were captured in the St. Lawrence River during the course of their catadromous migration to the breeding area located in the Sargasso Sea.

Chemistry

Chemical analyses were run on 15 organochlorine contaminants listed in Table 2. Upon arrival at the laboratory, the eels were gutted, and their heads and caudal fins were removed. They were then homogenized in a meat grinder and frozen until the chemical analyses were conducted. Five-gram homogenates were extracted with a mixture of acetone–hexane (1:1) and 5 g of anhydrous sodium sulfate. Filtered organic extracts were evaporated to near dryness and redissolved in ethyl acetate. They were then centrifuged (5 min) and purified by permeation gel chromatography using a 30 cm × 3 cm Bio-beads SX-4 column. Dried eluates were further purified by 2% water deactivation Florisil chromatography (20 cm × 1 cm column). Fraction i (hexane) yielded HCB, DDE, PCB, and mirex. Fraction ii (mixture of hexane–acetonitrite–dichloroethane (50.0:0.35:49.65)) yielded the other contaminants (see Table 2).

Fractions i and ii were analysed by gas–liquid chromatography with packed columns for PCB and capillary columns for the other contaminants. The carrier gas was argon–methane (95:5, 30 mL·min^{-1}) in the packed columns (1.95% OV-17 + 2.65% OV-210, HP chromosorb mesh 80/100) and helium (1 mL·min^{-1}) in the capillary columns (DB-1 or SE-52 methyl silicone, HP-1 cross linked fused silica). Electron capture detectors (25 and 15 millicuries for packed and capillary columns, respectively) at 350°C were used with argon–methane (95:5) as make up gas in both types of columns. PCB were measured as described by Reynolds (1971) (DDE relative retention time (RRT_{DDE}) 147, 177, and 210). RRT_{aldrin} and external standard methods were used for the other contaminants. Mirex was confirmed by either a nitration technique (Holdrinet 1979) or UV irradiation (Mes et al. 1978).

Contaminant levels are expressed in nanograms per gram of wet weight. The detection limit was 10 ng·g^{-1} for PCB and 1 ng·g^{-1} for the other contaminants. Values that fell below the detection level were considered as zeros. Precision and accuracy of the analytical methods are checked periodically through a Federal Interdepartmental Check Program and the International Atomic Energy Agency.

Statistical Analyses

In order to study the variability in contamination levels among the six groups of eels, principal component analyses (PCA) of

TABLE 2. Means and standard deviations of contaminant concentrations ($ng \cdot g^{-1}$). Contaminants are listed according to the order of elution in two fractions.

Contaminant	Group					
	KAM	QUE	SPN	SPS	SPI	RIC
HCB[a]	53 ± 43	43 ± 62	36 ± 34	34 ± 41	5 ± 3	7 ± 4
PCB[a]	6320 ± 4320	5624 ± 4910	4491 ± 3733	3195 ± 2822	981 ± 679	2555 ± 2476
Mirex	195 ± 195	112 ± 202	118 ± 111	64 ± 110	2 ± 4	0.1 ± 0.6
α-BHC[a]	14 ± 14	16 ± 10	23 ± 23	61 ± 56	39 ± 24	30 ± 28
Lindane	4 ± 14	11 ± 26	13 ± 22	44 ± 70	4 ± 4	6 ± 9
Aldrin	2 ± 4	35 ± 76	22 ± 22	80 ± 77	31 ± 23	20 ± 12
Heptachlor	6 ± 13	12 ± 17	25 ± 45	26 ± 40	7 ± 3	26 ± 33
H. Epoxide[a]	2 ± 5	11 ± 9	11 ± 11	43 ± 52	1 ± 3	9 ± 8
γ-Chlordane	1 ± 5	7 ± 27	10 ± 17	36 ± 82	5 ± 6	6 ± 11
Oxychlordane	13 ± 14	9 ± 19	12 ± 15	23 ± 40	8 ± 7	8 ± 9
Dieldrin	18 ± 39	25 ± 38	87 ± 105	129 ± 132	35 ± 36	39 ± 33
Endrin	0.4 ± 3	1 ± 6	33 ± 60	66 ± 164	15 ± 40	2 ± 5
DDD[a]	184 ± 162	140 ± 116	118 ± 106	176 ± 208	23 ± 23	186 ± 401
DDE[a]	753 ± 669	381 ± 405	462 ± 365	247 ± 270	253 ± 180	376 ± 353
DDT[a]	141 ± 138	107 ± 137	68 ± 84	148 ± 207	6 ± 15	190 ± 263

[a]α-BHC = benzene hexachloride; DDD = dichloro–diphenyl dichloroethane; DDE = dichloro–diphenyl dichloroethylene; DDT = dichloro–diphenyl trichloroethane; H. Epoxide = heptachlor epoxide; HCB = hexachlorobenzene; PCB = polychlorinated biphenyls.

TABLE 3. Proportion of fish from each group that the discriminant analysis reclassified in each group according to their contaminant levels[a]

Group	Sample size	Percent reclassified into group					
		KAM	QUE	SPN	SPS	SPI	RIC
KAM	104	61	23	7	0	6	4
QUE	127	10	65	9	2	6	9
SPN	52	8	12	60	2	12	8
SPS	32	0	13	6	63	19	0
SPI	8	0	13	0	0	88	0
RIC	40	5	8	13	0	13	63

[a]The numbers of fish reported here are smaller for some groups than the numbers reported in Table 1 because some fish were rejected from the discriminant analysis due to missing contaminant data.

the concentrations of the 15 pesticides and of total body length were computed. Multivariate methods represent the dispersion of objects (in this case eels) in a multidimensional space that includes as many axes as there are variables (in this case pesticides). PCA allow an optimal representation of this dispersion of objects or of the variables (also called descriptors) in a reduced space defined by the principal components, which maximizes variability. The correlation between the descriptors and the principal components is proportional to their projection on the components.

PCA were conducted on the correlation matrix using eigenvectors with unit norms. The correlation matrix was chosen over the covariance matrix because variables of a different nature were analysed together (pesticide levels and length) (Legendre and Legendre 1984). A unit norm was preferred because our intent was to represent both the objects and the variables in the reduced space (Legendre and Legendre 1984). An equilibrium circle of descriptors indicated if the contribution of each contaminant to the reduced space was above or below what would be expected under a hypothesis of equal contribution of all descriptors.

The value of organochlorine contaminants as chemical markers of the geographic origin of eels was investigated with discriminant analyses. Discriminant analysis builds a set of linear combinations that best reveals the differences among the groups. The performance of the discriminant function is then evaluated by estimating the probability of correct reclassification of the objects into the groups defined by the discriminant function. The relative importance of each contaminant to the overall discrimination (expressed as the partial r^2) was examined with a stepwise discriminant analysis which selected in a forward manner a subset of contaminants to produce the best discrimination possible. All the multivariate analyses were performed with the statistical package SAS (SAS Institute Inc. 1987). Total DDT (DDD + DDE + DDT) was used as a sixteenth variable in the multivariate analyses.

Results

The overall contamination level of SPS eels was the highest as they had the highest mean contaminant concentration of all the groups for nine of the contaminants (Table 2). By contrast, KAM eels and SPI eels, each had the lowest mean concentration of all the groups for seven and eight of the contaminants, respectively (Table 2).

A discriminant analysis reclassified eels into groups according to their contaminant patterns: of the two groups that had known geographic origins, most SPI eels (88%) and 63% of RIC eels were reclassified into their correct group (Table 3). Although the remaining groups had unknown and probably heterogeneous geographic origins, the percentages of reclassification of the discriminant analysis into the correct groups remained fairly high, around 60% (Table 3).

The proportion of the total variance explained by the first and the second principal components were 0.30 and 0.18, respectively. According to the broken stick model of Frontier (1976), only the eigenvalues of the first two components were above what would be expected from random. DDD, DDE, DDT, total DDT, HCB, PCB, mirex, and body length com-

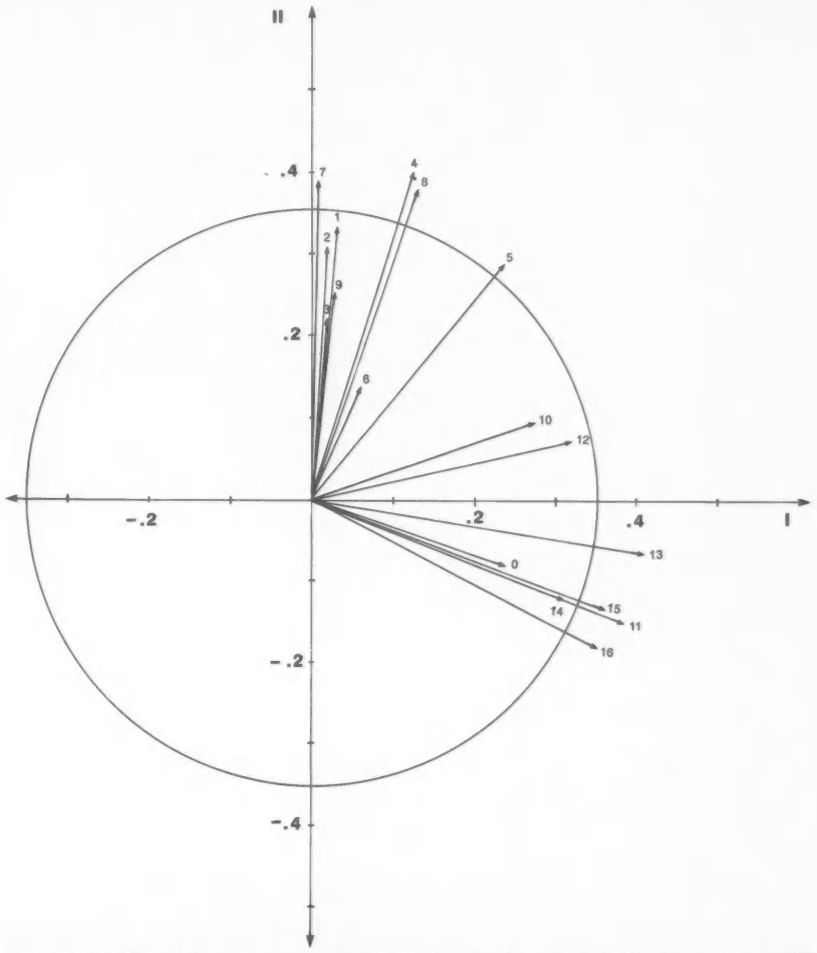

FIG. 2. Contribution of each contaminant to the two principal components (0 = length, 1 = α-BHC, 2 = lindane, 3 = heptachlor, 4 = heptachlor epoxide, 5 = oxychlordane, 6 = γ-chlordane, 7 = aldrin, 8 = dieldrin, 9 = endrin, 10 = DDD, 11 = DDE, 12 = DDT, 13 = total-DDT, 14 = HCB, 15 = BPC, 16 = mirex). The equilibrium circle of descriptors indicates if the descriptors are above (vector reaches circle) or below (vector does not reach circle) what would be expected under a hypothesis of equal contribution of the descriptors.

prised the first principal component (Fig. 2). Length contribution to the first component was not important as its projection on that component was the smallest of the descriptors that contributed to the first component. The rest of the contaminants contributed to the second component.

PCA showed that most eels that presented an unusual contaminant pattern were captured in Lake Saint-Pierre south (group 4 of Fig. 3). The separation of outlier SPS eels from the main distribution was mostly on the second principal component. Because we assumed that eels with mirex had a common geographic origin (Lake Ontario), we then calculated a PCA restricted to eels that had mirex, which showed that outlier SPS eels were still present (Fig. 4). Moreover outlier SPS eels were also found when only eels without mirex were analysed (Fig. 5).

Heptachlor epoxide, with a partial coefficient of determination (partial r^2) of 0.28, was by far the contaminant that contributed the most to the discrimination between groups (Table 4). Mirex contribution to the discrimination was only marginal. Three contaminants (lindane, DDD, and HCB) did not meet the significance criterion for inclusion in the stepwise discriminant analysis ($p > 0.05$).

Discussion

The relatively high discrimination among eels from various sampling sites, based on their contamination levels, indicates that samples of these migrating fish caught at upstream locations differed from those captured at downstream locations. This apparent spatial change in overall contaminant pattern may have two causes: the additions of animals from various tributaries along the St. Lawrence River and/or differences in sampling dates between stations which would result in catches of fish from different origins. Size differences among groups do not seem to account for differences in levels of pesticides, except

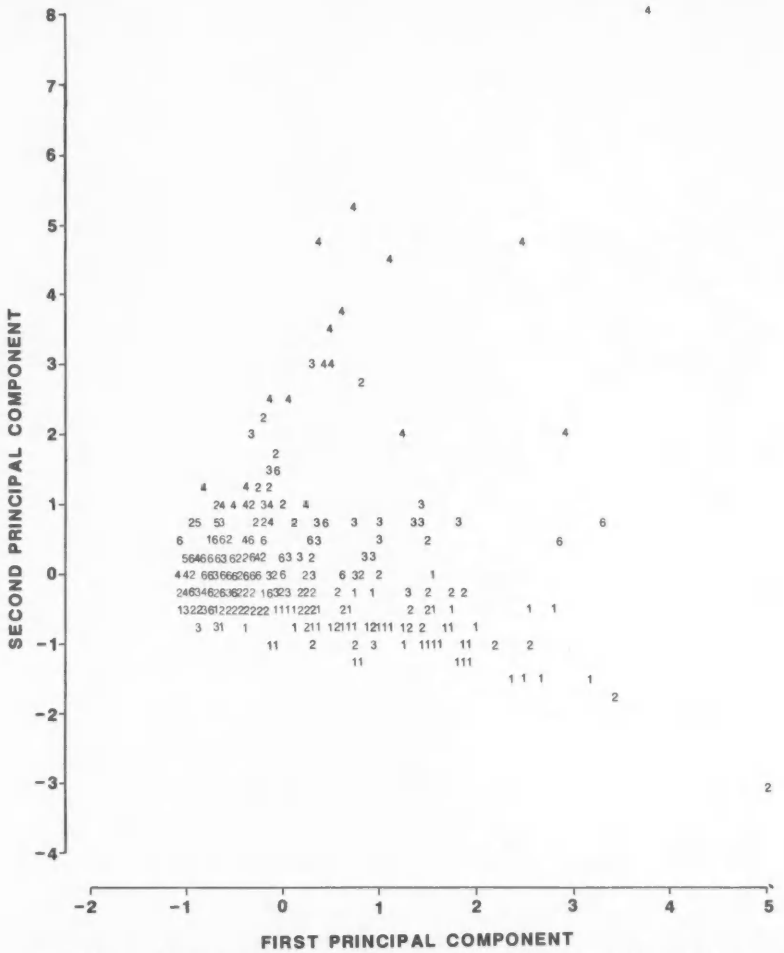

FIG. 3. Position of individual eels from the different groups (1 = KAM, 2 = QUE, 3 = SPN, 4 = SPS, 5 = SPI, 6 = RIC) in the reduced space defined by the two principal components. One hundred and fifty overlapping observations are hidden.

for SPI eels. In this group, size differences probably explain part of the high discrimination (as well as the low contamination level) as smaller and hence younger immature fish are likely to be less contaminated.

Dutil et al. (1985) concluded that eels with mirex represented one stock (Lake Ontario stock) while eels without mirex were a stock composite. By contrast, the similarities of distributions of eels with and without mirex on the first two principal components and the low contribution of mirex to the stepwise discriminant analysis, reported in this study, argue that mirex presence/absence does not allow such a distinction.

The presence of outlier SPS eels when the PCA was limited to eels that had mirex was unexpected because we were assuming that all eels with mirex had a common geographic origin, Lake Ontario. Should this have been the case, the presence of outlier SPS eels would not have occurred so markedly when the analysis was restricted to eels that had mirex. The similarity between plots of animals with or without mirex with respect to outlier SPS eels suggested these outlier SPS eels had a common geographic origin, different from most other eels, whether or not they had mirex.

The evidence presented above is hard to reconcile with current knowledge of mirex distribution; it indicates that contamination of eels with mirex is not restricted to Lake Ontario. It also provides a more likely explanation for the occurrence of mirex in immature eels from Lake Saint-Pierre than what Dutil et al. (1985) had proposed, as it seems unlikely that immature eels could have accomplished the extensive movements that their interpretation required.

To add weight to the above evidence on mirex distribution, the contaminant levels of a fish species of Lake Saint-Pierre (the Lake sturgeon) were measured. Mirex was detected in 64 of 77 sturgeons analysed in 1985 and in 17 of 68 sturgeons analysed in 1986 with a mean ($\pm$ SD) concentration of 11 $ng \cdot g^{-1}$ ($\pm$ 10) for 1985 and of 2 $ng \cdot g^{-1}$ ($\pm$ 4) for 1986. This strongly suggests that mirex is present in Lake Saint-Pierre, although we can provide no explanation for the different levels of mirex contamination between 1985 and 1986. The upstream portion of Lake Saint-Pierre represents one of the most important zones

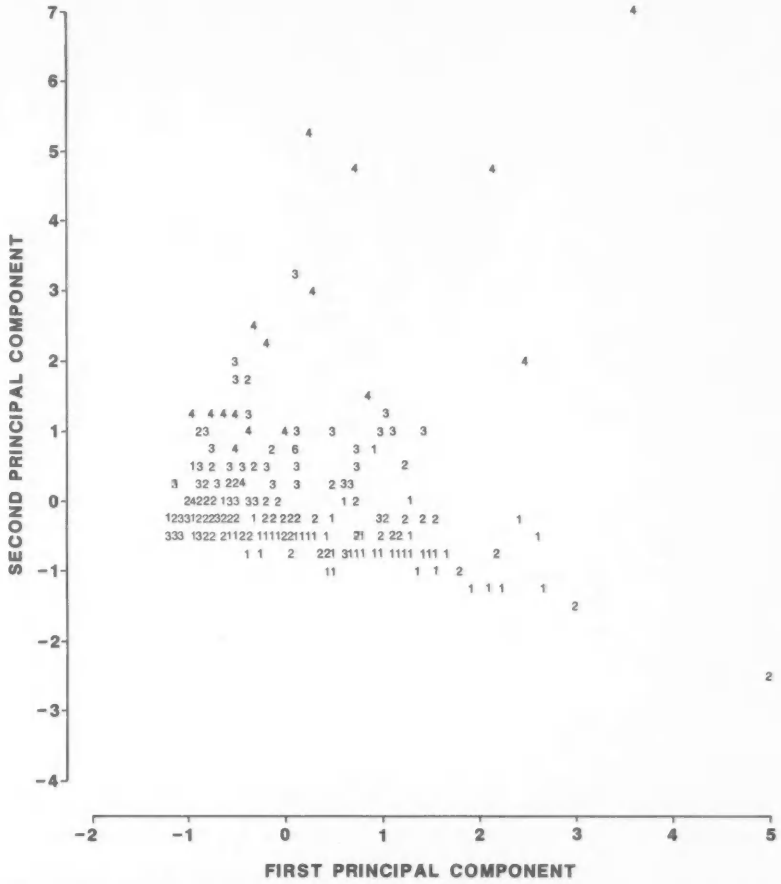

FIG. 4. Position of individual eels from the different groups (1 = KAM, 2 = QUE, 3 = SPN, 4 = SPS, 5 = SPI, 6 = RIC) in the reduced space defined by the two principal components when only eels with mirex were considered. Eighty-five overlapping observations are hidden.

of accumulation of pollutants in the St. Lawrence River (Couillard 1982).

Considering the insolubility of mirex in water (Alley 1973) and the absence of evidence for atmospheric transport of this pollutant (Strachan et al. 1980), it appears that the only way mirex could have been transported downstream to Lake Saint-Pierre is in the suspended sediments. Levels of 6 $ng \cdot g^{-1}$ of mirex have been measured in particulate matter exiting Lake Ontario (Lum et al. 1987). Therefore, it appears to have taken less than 14–19 yr (between 1963–68 and 1982) for Lake Ontario mirex-contaminated sediments to be transported downstream for a distance of at least 400 km. The possibility that these sediments drifted further downstream remains to be investigated.

Dutil et al. (1985) estimated that Lake Ontario eels do represent over 70% of the eels caught in the St. Lawrence River fishery. This proportion was probably overestimated because they assumed that all eels with mirex came from Lake Ontario. The present study shows that eels originating from the St. Lawrence River itself, from its source down to Lake Saint-Pierre (and maybe further downstream) may have presented detectable levels of mirex that resulted in their incorrect designation as Lake Ontario eels. Therefore data on presence/absence of mirex, such as shown in Table 1, allow a distinction between eels originating from the Lake Ontario/St. Lawrence River axis and eels coming from tributaries of the St. Lawrence River.

Comparing the distributions of eels on the two principal components also revealed that contaminant patterns of maturing eels differed between the northern and the southern side of Lake Saint-Pierre. This geographic difference was further exemplified with the discriminant analysis. Only one out of 52 eels from SPN was reclassified into SPS and only two out of 32 eels from SPS were regrouped into SPN. Differences in contaminant levels among animals migrating down Lake Saint-Pierre indicate that eels that migrate on the northern side of Lake Saint-Pierre have a different geographic origin than eels migrating on the southern side of the lake. This difference could be related to the hydrographic regime of the Lake. We suggest that eels migrating on the northern side of Lake Saint-Pierre come mostly from Lake Ontario whereas fish migrating on the southern side mostly originate from an unknown highly polluted area of the St. Lawrence River.

This study demonstrates that valuable information regarding fish stock discrimination and environmental distribution of con-

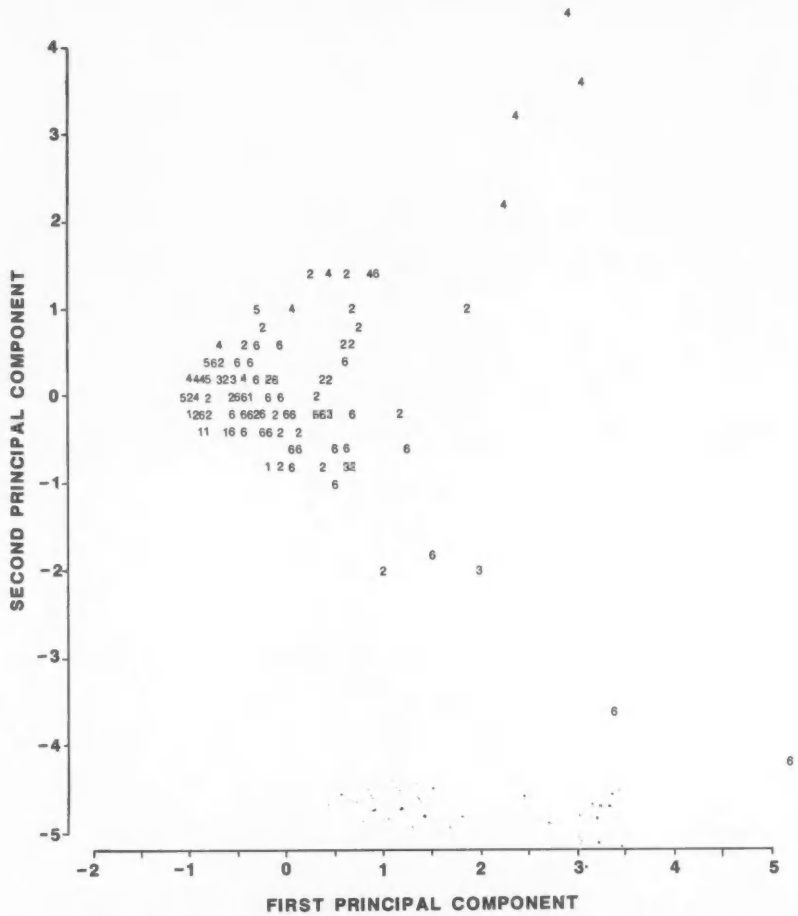

FIG. 5. Position of individual eels from the different groups (1 = KAM, 2 = QUE, 3 = SPN, 4 = SPS, 5 = SPI, 6 = RIC) in the reduced space defined by the two principal components when only eels without mirex were considered. Twenty-five overlapping observations are hidden.

TABLE 4. Importance of individual contaminants to the discrimination between groups as shown by the partial r^2 of a stepwise discriminant analysis. Significant contaminants ($p < 0.05$) are listed in decreasing order of importance.

Contaminant	Partial r^2
Heptachlor epoxide	0.28
α-BHC	0.18
DDE	0.16
BPC	0.14
Dieldrin	0.13
Endrin	0.10
Heptachlor	0.09
DDT	0.09
γ-Chlordane	0.06
Oxychlordane	0.04
Aldrin	0.05
Mirex	0.03

taminants can be gained by comparing organic contaminant levels among groups of fish. We believe that this method of stock discrimination could be successfully applied to other fisheries problems. It could for example enable fisheries managers to distinguish between stocks (or at least regions or countries of origin) in oceanic salmon fisheries.

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Hydraulic Geometry in Small, Coastal Streams: Progress Toward Quantification of Salmonid Habitat

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Hogan, D. L., and M. Church. 1989. Hydraulic geometry in small, coastal streams: progress toward quantification of salmonid habitat. Can. J. Fish. Aquat. Sci. 46: 844–852.

It is difficult to quantify in-stream physical attributes of salmonid habitats, yet quantification is necessary if conditions are to be compared within or between streams over time or space. This paper presents an objective method based on hydraulic geometry to quantify hydraulic characteristics of fish habitat. Two small streams in coastal British Columbia provide examples. Morphological mapping and streamflow measurements were used to generate the bivariate distributions of mean depth and mean velocity at cross sections within the study reaches at various discharges. The distributions are used to generate measures of potentially useable area within the streams. Survey criteria and numerical adjustments are presented to improve comparability between channels. The streams respond similarly to a change in discharge. The main hydraulic difference is a decrease in area useful to coho salmon (*Oncorhynchus kisutch*) for rearing at higher discharges in Bonanza Creek (logged) compared with Hangover Creek (unlogged). The example indicates that quantitative comparisons can be made, at comparable flows, between reaches and between streams, or over time.

Il est difficile de quantifier les attributs physiques des habitats des salmonidés dans les cours d'eau, mais il est nécessaire de le faire pour comparer les conditions qui existent dans un cours d'eau ou entre les cours d'eau en fonction du temps et de l'espace. Le présent article présente une méthode objective basée sur la géométrie hydraulique pour quantifier les propriétés hydrauliques de l'habitat des poissons. Deux petits cours d'eau de la côte de la Colombie-Britannique ont servi d'exemples. On a utilisé la cartographie morphologique et des mesures d'écoulement pour générer des distributions à deux variables de la profondeur moyenne et de la vélocité moyenne à certaines intersections des tronçons étudié à divers débits. Les distributions servent à générer des mesures de zones utilisables dans les cours d'eau. On présente des critères d'enquête et des facteurs de correction ayant pour but de mieux comparer les données provenant de divers canaux. Les cours d'eau répondent de la même façon à une modification du débit. La principale différence hydraulique est une diminution de la zone utile pour l'engraissement du saumon coho (*Oncorhynchus kisutch*) à des débits plus élevées à Bonanza Creek (forêt exploitée) qu'à Hangover Creek (forêt non exploitée). L'exemple indique qu'on peut faire des comparaisons quantitatives, à des débits comparables, entre des tronçons et des cours d'eaux, ou en fonction du temps.

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The freshwater physical habitat of salmonids has proven difficult to quantify with precison. While there is wide agreement that the occurrence and density of stream biota are controlled by flow regime, channel substrate, channel cover, water quality and biotic interactions, there appears to be little consensus about effective methods to collect and analyse relevant information for habitat assessments or comparisons. Methods of "habitat" characterization vary from specification of summary flow regime data (e.g. Tennant 1976) through more detailed hydrological, hydraulic, and physical environment descriptions (e.g. Collings et al. 1972), to full habitat inventory schemes (e.g. DeLeeuw 1981; Bisson et al. 1982) that include biotic factors. Habitat inventory schemes have been extended to provide quantitative means for estimating fish standing crops or carrying capacity (cf. Binns and Eiserman 1979). This obviously is a desirable goal in habitat assessments.

Summary flow regime data ignore limiting conditions such as minimum depth for fish passage, access to cover, or the occurrence of excessive velocities, and therefore are unsatisfactory for describing physical habitat. Detailed physical environment descriptions can identify such factors, but they do not provide anything like a complete habitat description. A detailed habitat inventory appears to be the only basis for predicting stream carrying capacity or standing crop. However, a comparison of empirical models (cf Binns and Eiserman 1979; Bowlby and Roff 1986) shows that they are only regionally valid, at best, and may vary dramatically in form because different aspects of habitat become the critical, limiting elements for particular species in different regions, or even in different streams within a region.

Nonetheless, hydrological and hydraulic properties of stream channels remain important elements of habitat: they define the "potentially useable area" in the stream. A thorough description must include their relationship with channel morphology. This is achieved in the "hydraulic geometry" of the stream channel. Hydraulic geometry describes the effects of flow variability on the dimensions and velocity of the stream consistently and repeatably. Mosley (1983) made some notable inno-

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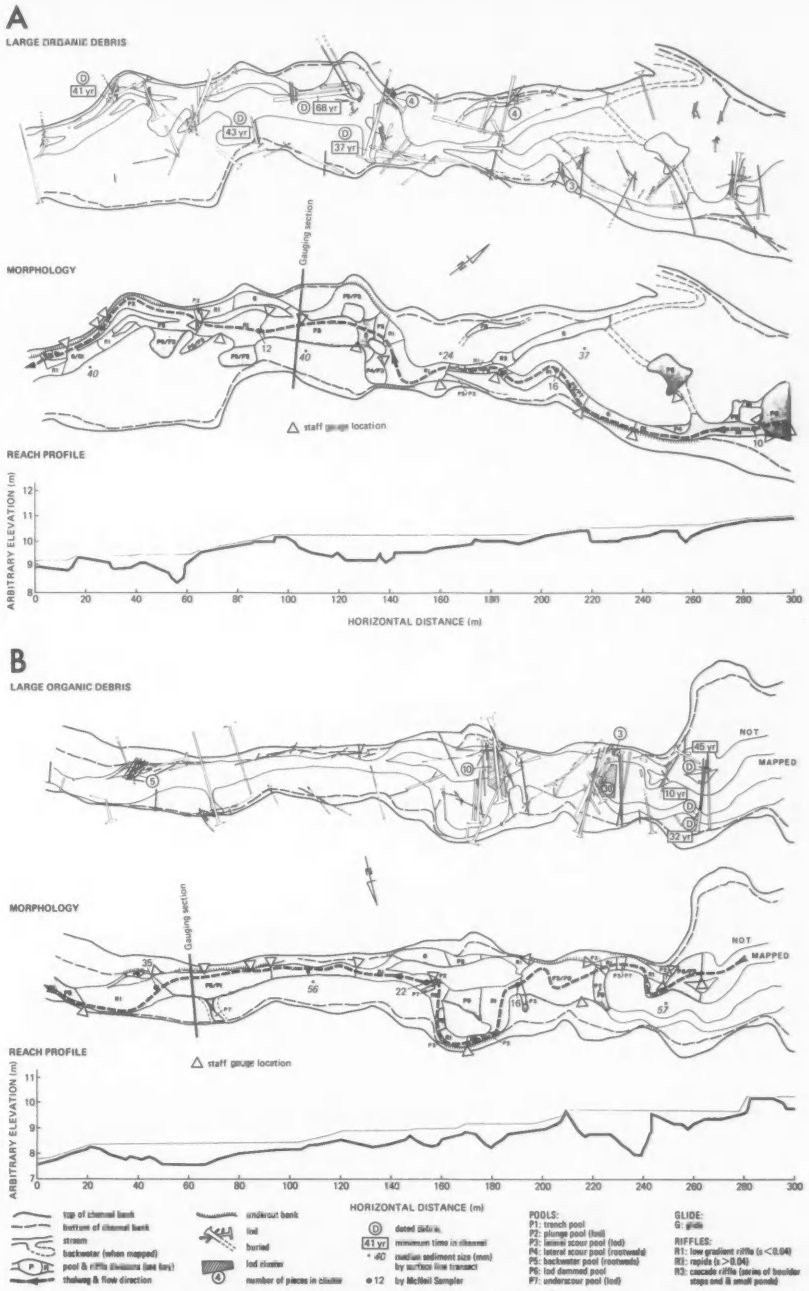

FIG. 1. Morphology and long profiles of the study reaches, including measurement section locations. (A) Bonanza Creek, (B) Hangover Creek; includes legend.

vations in presentation of hydraulic geometry for application to the study of habitat distribution in a large, braided river channel. Nevertheless, there remains substantial scope for extending the application of hydraulic geometry in the analysis of fish habitat.

The specific objectives of this paper are: (1) to present an objective method of quantifying hydraulic conditions to enable assessment of potentially useable areas in stream channels; and (2) to demonstrate the application of hydraulic geometry to effect meaningful comparisons between streams, or between different surveys within the same stream.

The field data used to address the study objectives were obtained from two small streams on the west coast of the Queen Charlotte Islands, British Columbia. This area is considered

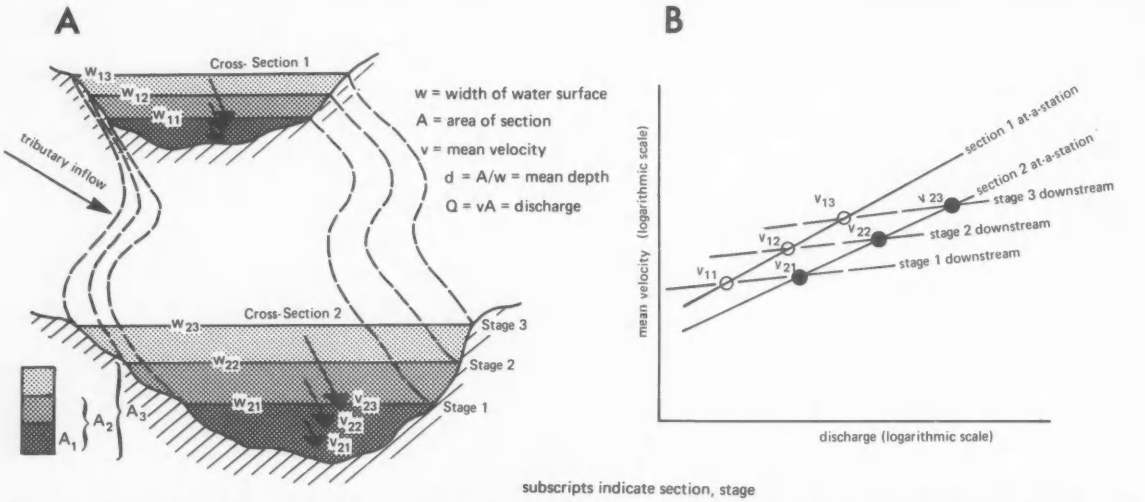

FIG. 2. Definition diagram for hydraulic geometry of a stream channel. (A) Two cross-sections of a stream separated by the entry of a tributary, showing width at the water surface (w), a proportional representation of velocity (v, arrows), and area (A, shaded) at three stage levels (discharges). The broken lines are idealized bank lines to indicate that stages 1 to 3 correspond in frequency of occurrence between the two cross-sections. (B) Graph on logarithmic axes of cross-section properties in (A), plotted against discharge. The notation is for mean velocity (v). Channel width, mean depth, and cross-section area exhibit the same functional dependence. The "downstream" relations (joining sets of points plotted at corresponding stage along the channel) are extrapolated to indicate that the fundamental relation persists for a substantial distance along the channel.

typical of much of coastal British Columbia. The study sites have been described previously by Hogan (1986) and the morphology of each study reach is shown in Fig. 1. Comparison of many morphological parameters, including pool, riffle, and bar character, sediment size, bank configuration, and large organic debris, indicates that the two streams are very similar. The mean bankfull width is about 50% greater in Bonanza Creek than in Hangover Creek. Sediment textures are predominantly gravel, cobble, and sand.

Hydraulic Geometry

The "hydraulic geometry" of a stream channel (Fig. 2) describes the change in water surface width (w), mean depth (d), and mean velocity (v) as discharge (Q) changes over time at a single cross-section ("at-a-station" hydraulic geometry), or downstream as drainage area increases ("downstream" hydraulic geometry) (Leopold and Maddock 1953). Downstream hydraulic geometry relates changes in w, d and v at sites located progressively downstream to a reference flow which increases according to the increase in drainage basin area and runoff. The reference flow is one that recurs with the same frequency (for example, mean annual flood) at all stations.

Hydraulic geometries are conventionally expressed as simple power functions, as follows (see Fig. 3):

$$(1)\quad w = aQ^b$$

$$(2)\quad d = cQ^f$$

$$(3)\quad v = kQ^m$$

$$(4)\quad A = tQ^p = acQ^{b+f}$$

The principal quantities are defined in Fig. 2. The exponents (b, f, m, t) and the coefficients (a, c, k, p) customarily are derived statistically. From the continuity equation, $Q = wdv$, it is evident that the exponents in equations (1)–(3) must sum to unity and the coefficients must have a product of unity, hence there are only two independent relations.

At-a-station hydraulic geometry provides a concise description of the variation in channel geometry and flow velocity as the flow varies. The at-a-station hydraulic geometry for Bonanza Creek (Fig. 3a) is described by single power functions, but there is a break near $Q = 1.0\ m^3 \cdot s^{-1}$ in the Hangover Creek plots (Fig. 3b). The reason for this is apparent in the accompanying cross-section which indicates that channel shape is important. As flows increase, width increases quickly on the left side until it approaches 20 m. After this the rate of increase is reduced as discharge increases. Conversely, as the flow width approaches 20 m the rate of change in depth increases as the left bank steepens. As discharge increases, the largest corresponding adjustment occurs in velocity. Width and depth increase at a slower rate. Although these relations provide specific hydraulic information, they represent only summary conditions for one cross-section within a single stream. Extrapolation to different cross-sections is not appropriate. Yet such at-a-station relations, which can be developed from stream gauging data, are often the only quantitative hydraulic data available for fisheries studies.

Downstream hydraulic geometry provides a basis upon which to estimate the summary hydraulic conditions at various locations within the stream system. Downstream relations were not developed in the present study, but previous work has shown that they are relatively consistent (Ferguson 1986). General studies of hydraulic geometry indicate that there may exist two basic behaviors based on the depth exponent, respectively $f = 0.33$ and $f = 0.40$, depending upon relative sediment mobility. The width exponent in the downstream case always has $b \sim 0.5$. Coefficients depend upon bed and bank materials, but a single gauging station serves to specify values for a stream system.

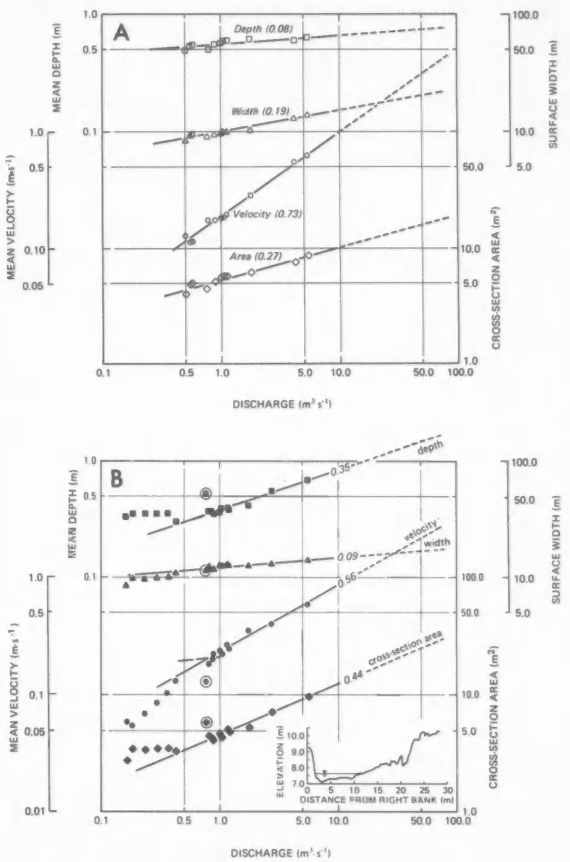

FIG. 3. At-a-station hydraulic geometry based upon gauging measurements in (A) Bonanza Creek and, (B) Hangover Creek. Note the departure of the data of the "at-a-station" hydraulic geometry from simple form near $Q = 1.0\ m^3 \cdot s^{-1}$: see text for discussion. The aberrant circled point (B, d high; v low) at $Q = 0.85\ m^3 \cdot s^{-1}$ is not unusual: it would be produced by transient conditions such as a temporary blockage of the channel downstream by wood debris. Inset: channel shape in the measurement section.

Thus it is possible to use published relations to estimate channel width, mean depth, and mean velocity at different locations along the channel, for some specified flow level, once a single gauging section has been established.

In summary, at-a-station relations describe hydraulic conditions for a range of discharges at one site and downstream relations provide information for different locations at a specified flow level. They do not provide details of local variability within a section.

An extension of at-a-station hydraulic geometry combines information from a number of cross-sections within a single reach of the channel, or from a selected major habitat unit. A reach is a length of stream channel with homogeneous morphological, sedimentological, and hydrological features. Habitat units (cf. Fig. 1) include pools, riffles, and glides, and form the basic morphological components of a reach (see Bisson et al. 1982). The values of the hydraulic parameters at all cross-sections may be tabulated to indicate the variation that occurs between individual sections within a reach (or within a habitat unit). Alternatively, they may be averaged to specify a mean hydraulic geometry for the reach or habitat unit. These procedures form the basis for the application of hydraulic geometry to achieve the objectives of this paper.

Methods

The field work consisted of two main tasks. The first was to survey a detailed topographic map of each reach and the second was to obtain the streamflow hydrographs for both reaches. Integration of these morphological and hydrologic elements is described below.

Field methods involved standard streamflow gauging (Church and Kellerhals 1970; Platts et al. 1983) and channel mapping techniques for small channels. Topographic surveys were conducted with a theodolite, stadia rod, and fibre measuring tape. This included cross-sectional transects spaced approximately 10 m apart along the channel and a longitudinal profile of thalweg elevation. All morphological, sedimentological, and vegetation changes of interest were located in the survey. Also, all major channel features located between the cross-sections were surveyed. These included the position (horizontal and vertical), shape (lateral and longitudinal extent) and orientation of all pool–riffle breaks, bar surfaces and side and back channel features. A topographic map was drawn at a scale of 1:200 on the basis of the survey data and ground photographs.

Stream discharge for each reach was determined at a surveyed cross-section located in a pool, approximately one-third of the pool length upstream from the riffle–pool break (Fig. 1). Elevations were surveyed at 0.3-m intervals across the channel to define the gauging section. The cross-section was resurveyed at several stages and the water surface width, water depths, and flow velocities were measured. Velocity was measured at 4/10 depth if the flow depth was less than 1 m and at 2/10 and 8/10 when it exceeded 1 m. A Price type A current meter was used except during very low flows, when a small Ott meter was employed. Discharge measurements were made on 17 and 11 occasions in Hangover and Bonanza, respectively.

A new method is applied here to calculate the distribution of hydraulic parameters along the channel, hence, hydraulic habitat quantities, at different streamflow stages. A series of staff gauges was installed in each study reach (Fig. 1). These were located at topographic breaks separating habitat units. A level survey was conducted to tie all staff gauges to the reference staff gauge at the streamflow measurement section. The stage height at each gauge was read (± 1 mm) during every site visit. These water surface elevations were drawn onto a copy of the contour map after each visit. The discharge for the stream reach is known at all stages on the basis of the rating curve for the reference staff gauge. On the reasonable assumption that flow does not vary significantly within the reach during a survey, the mean velocity can be calculated for each cross-section at each stage as $v = Q/wd$, where discharge (Q) is known and water surface width (w) and mean depth (d) are obtained from the topographic map. This may produce some bias at low flow in certain riffle sections, where a significant proportion of the flow may occur through the streambed gravels below the bed surface. This would result in overestimates of open water discharges at these sites.

By measuring width and depth from the topographic map and calculating mean velocity at many cross-sections (spaced every 5 m along the reach maps, resulting in 53 and 62 cross-sections in Hangover and Bonanza, respectively) and interpolating

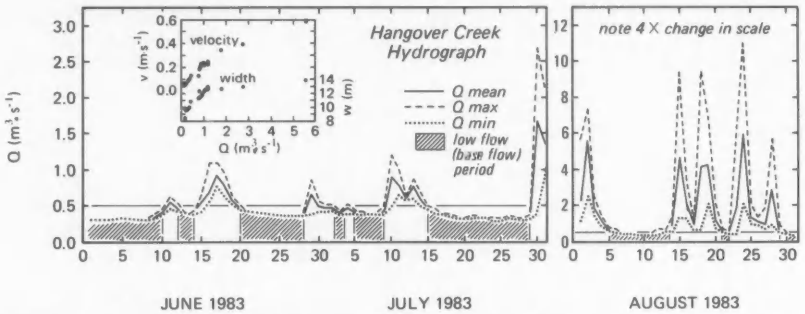

FIG. 4. Summer flow hydrograph in Hangover Creek, 1983. Low flow regime (<0.5 m^3·s^{-1}) is indicated. Note the 4× scale change in August. Inset: velocity and depth versus discharge. The clear break in these plots at $Q = 1.0$ m^3·s^{-1} is the same as that remarked in Fig. 3(B).

between cross-sections, an inventory was compiled of the amount (area) of channel which has specific mean depth and velocity characteristics. The same procedure was followed at different discharges enabling the sectional mean depth — mean velocity distributions at each stage to be calculated for each reach.

These results may also be averaged and then presented in the same manner as at-a-station results for a single section. We present reach averaged results below. These are useful to make certain adjustments to allow comparisons to be made between reaches, but in general this obscures variability of primary interest in habitat studies. In our study, there are a sufficient number of cross-sections to allow hydraulic conditions within specific habitat units to be studied as well.

Stream Stage and Channel Dimensions

Many observations made in the course of habitat inventories, such as extent of pools and riffles, extent of bank overhang, and total accessible bed area, are stage dependent. For valid comparisons to be made within the same reach over time, discharge should be the same during repeat inventories. Further, if comparisons between different reaches are to be valid, it is necessary that the comparison be restricted to flows with the same frequency of recurrence in the two reaches. (That is, between reach comparisons must be conducted under the same constraint as that noted for construction of "downstream" hydraulic geometry).

Because of the variable nature of streamflow and the paucity of gauging stations it is difficult to ensure that repeat surveys are conducted at the same flow. A possible solution is to make proportional adjustments of the channel dimensions according to the change in flow. Hangover Creek data are used to illustrate how a change in discharge affects channel dimensions typically measured in the field during habitat inventories. Figure 4 shows the summer discharge hydrograph for Hangover Creek. There is a wide range of discharges experienced during this period which is commonly designated the "summer low flow" period in coastal areas with minimal snowmelt runoff. The discharge ranges from approximately 0.3 to over 10 m^3·s^{-1}. The channel response is shown in the inset in Fig. 4. The response of width and velocity is not simply proportional across the range; a small change in discharge at the low flow end of the curve leads to a relatively large change in width and velocity. Conversely, at the high flow end of the curve, a large change in discharge leads to a relatively small change in width and velocity.

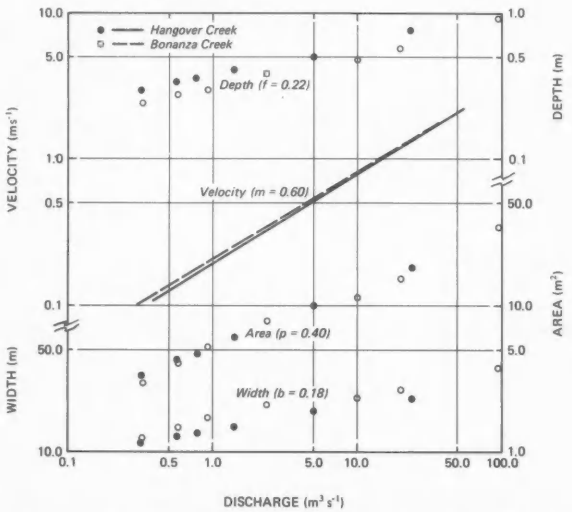

FIG. 5. Reach averaged "at-a-station" hydraulic geometries for Hangover (average of 53 cross-sections) and Bonanza (62 cross-sections) Creeks. Actual data are displayed except for velocity, which was computed from equations obtained for area. Closed symbols and solid lines indicate Hangover results.

A habitat biologist would wish to carry out a low flow inventory during the extended period of low flow in June and July. In Hangover Creek, flows of less than about 0.5 m^3·s^{-1} appear to represent "low flow." In this range, channel dimensions are most sensitive to changes in flow. The chance to obtain just the same flow in successive visits is not great. To obtain a proportional adjustment of channel properties we note as a general case from any of equations (1) to (4)

$$(5) \quad dx/dQ = yzQ^{y-1}$$

wherein x is any of the channel dimensions in those equations, and y, z are the at-a-station exponent and coefficient of the relation. Dividing through by the basic equation yields

$$(5a) \quad dx/x = ydQ/Q$$

that is, the proportional change in the channel dimension, x, between the two flows is equal to the hydraulic geometry exponent times the proportional change in discharge. We know that at-a-station exponents do not remain the same from reach to

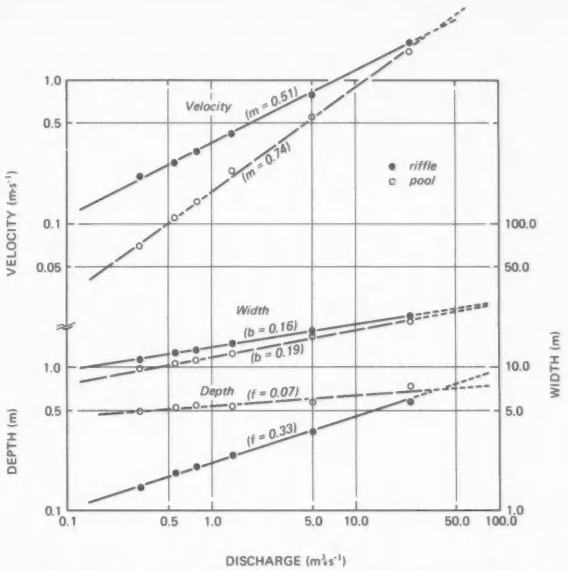

FIG. 6. Habitat averaged "at-a-station" hydraulic geometries for Hangover Creek for two major habitat units. Seven cross-sections were surveyed in a single pool and seven cross-sections on an adjacent riffle.

TABLE 1. Comparison of reach — averaged hydraulic geometry between surveyed reaches of Bonanza and Hangover Creeks[a].

Parameter[b]	Expected ratio[c]	Observed ratio[c]
Width (b = 0.5)	1.50	1.56
Depth (f = 0.4)	1.38	1.16
Velocity (m = 0.1)	1.08	2.20
Channel area (p = 0.9)	2.06	

[a]Ratio of drainage areas is 2.24.
[b]Values in brackets are downstream hydraulic geometry exponents suitable for gravel bed streams (Ferguson 1986).
[c]Ratio of Bonanza/Hangover.

reach (compare Fig. 3a and 3b), hence measurements are necessary to establish the hydraulic geometry. (However, it is not essential to have a continuous flow record so long as the flows at the times of survey are known).

As an example of an adjustment that might be made for a difference in flow between repeated surveys in the same reach, consider successive low-flow inventories in Hangover Creek at flows of 0.3 and 0.5 $m^3 \cdot s^{-1}$. For this adjustment, we use the reach-averaged hydraulic geometry displayed in Fig. 5. To standardize results on 0.5 $m^3 \cdot s^{-1}$ we require, for mean velocity (m = 0.60, from Fig. 5), $dv/v = 0.60(0.2/0.5) = 0.24$. Mean velocity in the 0.3 $m^3 \cdot s^{-1}$ survey should be increased by 24%. By a similar calculation, width should be increased by 7%. Using judgement, it may be reasonable to adjust other habitat quantities the values of which correlate strongly with these parameters.

Individual habitat types also display characteristically distinctive geometries. Figure 6 illustrates hydraulic geometries separately averaged for two main habitat types in Hangover Creek. Reach averaging within each habitat type ensures that purely local variations do not confuse the habitat appearances. The figure confirms intuition inasmuch as it shows that pools commence with relatively low velocities and high depth at low flow, and that these change to approach values found in riffles at high flow. In effect, the entire stream becomes more riffle-like, so the proportion of the stream represented by each habitat changes with flow. This defeats the assumption, sometimes made, that the proportion of each habitat type in each reach remains stable. It also makes it difficult to avoid bias in estimating habitat distributions if discharge changes significantly during a survey.

Reach-averaged hydraulic geometries, over all habitat types, are shown in Fig. 5 for both Hangover and Bonanza creeks. There appear to be only minor differences between the two streams. These may derive from subtle differences in bed and bank materials. However, they do reflect the difference that we would expect for increased sediment throughput as the result of logging (Lyons and Beschta 1983): Bonanza (logged) is somewhat wider, shallower, and faster at all flows. In a strict comparison, it is necessary to adjust for the different drainage areas. We must assume that the two reaches are equivalent regime types (that is, that bed and bank sediments have no significant differential effect on the channel form so that the coefficients in the downstream equations remain the same). Then from the downstream hydraulic geometry equations, we obtain (by dividing the equation for one stream by the equation for the other)

$$(6) \quad x_1/x_2 = (Q_1/Q_2)^y$$

Here, we assume further that $Q \propto A_d$, drainage basin area, so we estimate $x_1/x_2 \sim (A_{d1}/A_{d2})^y$, where x and y are as in equation (5), but for the downstream case. We obtain for the comparison Bonanza/Hangover, the results given in Table 1, which shows the expected ratios of mean hydraulic parameters based on the foregoing calculation procedure, and the observed ones. Bonanza Creek is substantially shallower and flows faster than expected.

The appearance that the larger (logged) channel is the shallower implies that the channel may be filling with sediment as a consequence of increased erosion and sediment transport. In the years after our 1983 surveys, the Bonanza reach has continued to become wider and shallower as the result of sediment filling the pools, so that a clear difference between the two channels is now evident.

Figures 5 and 6 include information that is useful in habitat evaluations. Since channel width essentially is substrate area per unit length of channel, the figures indicate how that habitat quantity varies, overall, with flow. They also provide an index of how quickly velocities increase in the channel as flow increases. Figure 5 provides the basis of a method to test for overall differences between reaches, or over time in one reach. Nonetheless, the conventional representation of hydraulic geometry shown in these figures gives only limited information for habitat studies since it is averaged over more or less well-defined units of the channel. It is useful to know the range of variability of the hydraulic properties of the stream.

Stream Stage and Velocity–Depth Distributions

Fish prefer specific hydraulic conditions during different phases of their life cycles. Therefore, the combination of depth and velocity at all locations within the study reach is important. Inventories of mean cross-section depth and velocity combinations for Hangover and Bonanza creeks have been compiled following the method of presentation developed by Mosley

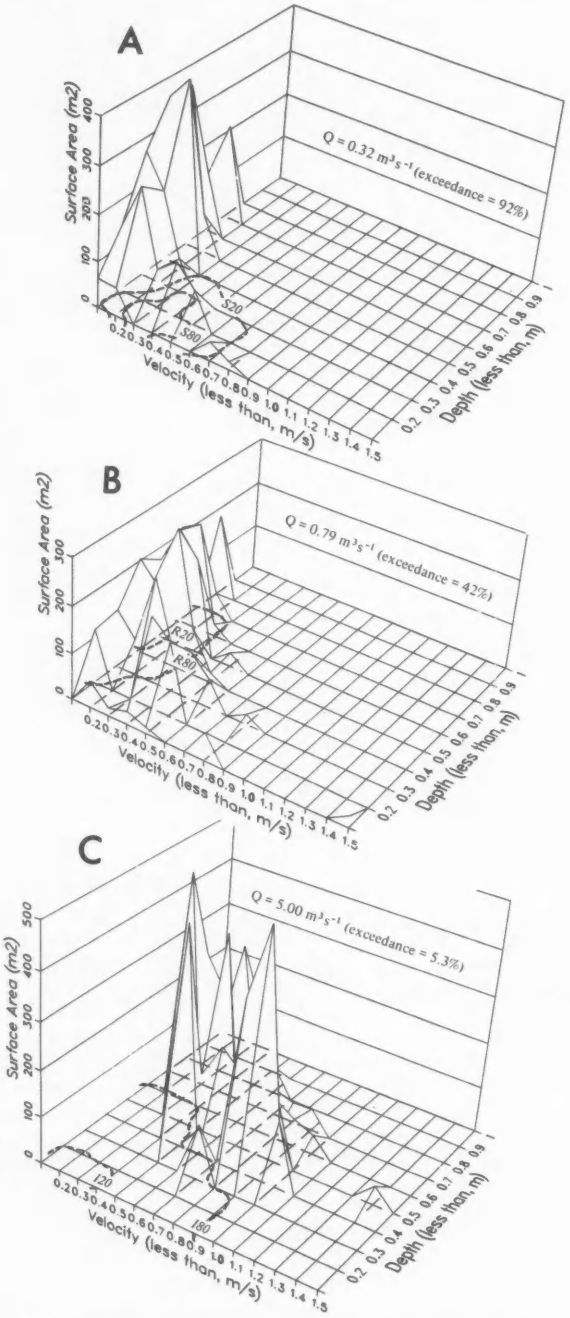

FIG. 7. Distribution of water surface area by depth–velocity class, classified in 0.1-unit intervals for three selected discharges in Hangover Creek. Bovee (1982) "probability-of-use" curves for *Oncorhynchus kisutch* added to the depth–velocity grid at 20 and 80% levels. I = incubation probabilities; S = spawning probabilities; R = rearing probabilities, shown in separate panels for clarity, but all are relevant in all panels. (A) $Q = 0.32\ m^3 \cdot s^{-1}$; flow exceedance 92% (B) $Q = 0.79\ m^3 \cdot s^{-1}$; flow exceedance 42% (C) $Q = 5.00\ m^3 \cdot s^{-1}$; flow exceedance 5.3%.

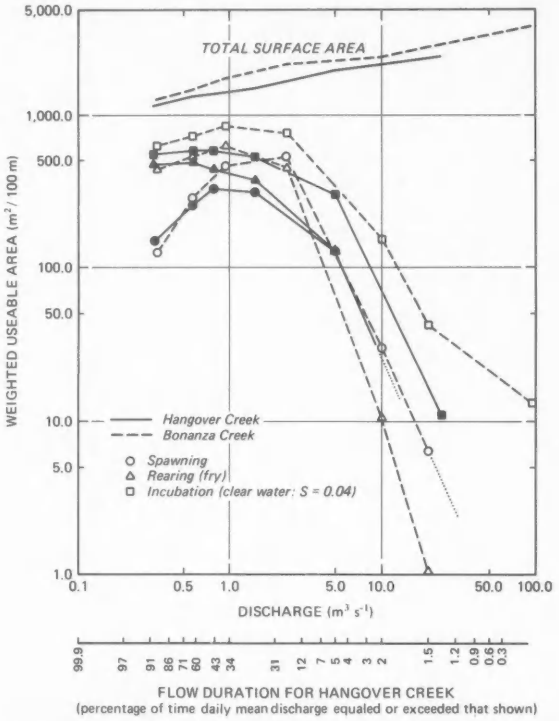
TOTAL SURFACE AREA
WEIGHTED USEABLE AREA (m2/100 m)
Hangover Creek
Bonanza Creek
Spawning
Rearing (fry)
Incubation (clear water: S = 0.04)
DISCHARGE (m3 s-1)
FLOW DURATION FOR HANGOVER CREEK
(percentage of time daily mean discharge equaled or exceeded that shown)

FIG. 8. Weighted useable areas for *Oncorhynchus kisutch* (square metres per 100 m of channel) for various flows (flow duration added for Hangover Creek).

(1982). The water surface areas in square metres, in increments of 0.1-m depth and 0.1 $m \cdot s^{-1}$ velocity, were calculated for a range of discharges. The entire study reach was used in both cases; this included 260 m in Hangover and 300 m in Bonanza. The discharges cover a range from the lowest recorded during the 1983 summer to the estimated bankfull discharge (extrapolated from morphological evidence and stage–discharge rating curves). This procedure provides a graphic demonstration of the overall change in water surface area with increasing discharge and the changing flow character (see examples in Fig. 7). We call this the "disaggregated hydraulic geometry."

The comparison of this information with habitat suitability criteria gives direct information about the quality of hydraulic habitat. For example, the "probability of use curves" of Bovee (1982) give depth–velocity combinations preferred by coho salmon (*Oncorhynchus kisutch*) for spawning, egg incubation, and fry rearing stages. (We note that a variety of criticisms has been made of Bovee's concepts (see Smith 1979), but they remain in wide use: we adopt them here as a convenient example.) The criteria are superimposed in Fig. 7.

At low flow conditions ($Q = 0.32\ m^3 \cdot s^{-1}$ in Hangover) the channel is composed primarily of relatively deep, slow moving water which is well suited to fry rearing (Fig. 7). Only a small proportion of the channel is well suited for spawning. As discharges increase there is a corresponding increase in overall water surface area and an increase in suitable spawning habitat. The relative area of rearing habitat begins to decline at $Q = 0.79\ m^3 \cdot s^{-1}$ in Hangover, since as discharge increases, velocity

increases at a faster rate than depth. As flow increases beyond about 5 $m^3 \cdot s^{-1}$ there is a progressive shift towards predominantly fast flowing, relatively deep water which is not suited for either spawning or rearing of fish.

Finally, a measure of channel area suitable on hydraulic criteria for use by coho salmon has been calculated and is presented in Fig. 8 for both streams. This was achieved by multiplying the water surface area of each depth–velocity class by its appropriate weighting factor from Bovee's (1982) "probability of use" curves. Summations of the weighted areas provide the total "weighted useable area" presented in the figure. Comparison of the two streams reveals that the larger Bonanza Creek retains less rearing area than Hangover Creek at flows greater than 4.0 $m^3 \cdot s^{-1}$ but has more incubation area at these flows. On a strictly proportional basis, it should have about 1.5 times as much habitat at all flows, but appears not to achieve this. The shallower, swifter flows in this stream dictate this outcome.

We emphasize that this measure represents hydraulically suitable area, or potentially useable area only (and only if the suitability for use criteria are appropriate). It does not measure habitat in toto since it ignores nonhydraulic factors such as bank cover or size of bottom gravel, and it certainly need not reflect actual use by fish. It nevertheless remains a useful measure of area potentially available under appropriate management.

Discussion and Conclusions

In this paper, we have presented hydraulic geometries of two small streams to assess their usefulness for fish habitat characterization. We have done this in two ways: (i) by presenting reach-averaged hydraulic geometry in conventional form for entire reaches (Fig. 5) and for specific habitat types (Fig. 6); (ii) by presenting depth–velocity distributions following techniques developed by M. P. Mosley, as the "disaggregated hydraulic geometry" of the reach (Fig. 7).

Both present useful information. The latter preserves important variability, and presents the significant joint distribution of the main hydraulic parameters. We have also stressed the importance of streamflow stage to the quantification of salmonid physical habitats.

Relatively small changes in stream discharge can lead to substantial changes in channel dimensions and, therefore, hydraulically defined habitat. Although the conventional representation of hydraulic geometry relations demonstrates this and provides flow information relevant to salmonid habitats, it has limited applicability because it expresses only summary conditions. Hence, conventional hydraulic geometries provide a poor basis both for quantifying habitat and for comparisons.

It is difficult to make exact estimates of channel area with suitable hydraulic conditions from the disaggregated results of Fig. 7, so a further display was developed of channel bed area having particular conditions estimated to be suitable for particular phases of fish development (Fig. 8). The information displayed is similar to that developed by Collings et al. (1972), but it is derived from hydraulic geometry and a detailed map, rather than from direct measurements at all flows. Hence, our data represent cross-section averages, whereas Collings et al. (1972) analyzed point measurements. Yet the number of measurements we have analyzed is about the same as the number of measurements they obtained and our reaches are 10 times as long. It is likely that we have sampled a more representative range of stream habitats. Our field effort was substantially less than that required by Collings et al. (1972). The method is objective and repeatable.

The averaging present in our results remains undesirable. It is a consequence of the computational means by which the results were derived. It will have reduced the range of the bivariate distributions (Fig. 7) below that which would be displayed by the full distribution of point values, and probably has changed the distributions modestly. Furthermore, it has been shown that fish are sensitive to velocities at specified distances from the streambed — the so called "nose velocity" (Smith 1979). This could be developed with information at hand if it were possible to adopt a suitable equation for the velocity profile (the map suffices to obtain point depths). This is feasible in large channels, but is not reasonable in small, relatively steep channels with very irregular boundaries. The alternative is to make velocity measurements at many places in the stream (as in Sullivan 1986). The advent of direct readout current meters make this less onerous than heretofore, but it remains an expensive, labour intensive task.

Alternately, it may be noted that the full distribution of actual velocities may be divided into two parts, the distribution about the mean velocity in the cross-section and the variation of the mean along the channel. It probably will always be impractical to obtain the full distribution by measurement in management studies, but it may be feasible to find and apply characteristic distributions for sections with specific morphology. Then it would be necessary only to determine variation in morphology and mean velocity along the channel, the result demonstrated in this paper.

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Changes in the Body Composition with Age of Goldeye, *Hiodon alosoides*

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Male goldeye, *Hiodon alosoides*, grew faster, matured earlier, and had a shorter lifespan than females as did exploited compared with unexploited populations. Instantaneous growth rates of the body organs and tissues were usually higher in the male than in the female. The proportion of fat to the total constituents in the muscle, liver, gut, and carcase of female and the gut and carcase of male goldeye declined with age while that in the ovary increased. The proportion of protein in the body tissues and organs of both sexes remained approximately constant with age. Ash content increased in the carcase of older females and males. Glycogen concentration in the liver varied extensively and was considered as indicator of stress and unrelated to aging processes. Between the ages of 10 and 16 yr the energy content of the female soma increased by 44% whereas the energy content of the ovary increased by 121%. The ovary selected essential fatty acids at the expense of the soma.

Les laquaiches mâles, *Hiodon alosoides*, ont une croissance plus rapide, arrivent plus tôt au stade adulte et vivent moins longtemps que les femelles, c'est aussi le cas des populations exploitées par rapport aux population non exploitées. Les vitesses de croissance instantanées des organes et des tissus de l'organisme étaient généralement plus élevées chez les mâles que chez les femelles. On a observé une diminution avec l'âge de la proportion de gras par rapport aux constituants totaux présents dans le muscle, le foie, l'intestin et la carcasse des femelles ainsi que dans l'intestin et la carcasse des laquaiches mâles; on a observé une augmentation de cette proportion dans les ovaires. La proportion de protéines dans les tissus et les organes des deux sexes est restée pratiquement constante avec l'âge. On a constaté une augmentation de la teneur en cendres dans la carcasse des femelles et des mâles plus âgés. La concentration de glycogène du foie était très variable et on estime qu'il s'agissait d'un indicateur du stress indépendant du processus de vieillissement. On a constaté un accroissement de la teneur énergétique du soma de femelles âgées de 10 à 16 an et un accroissement de 121 % de la teneur énergétique des ovaires. Les ovaires ont choisi des acides gras essentiels aux dépends du soma.

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In fish there is histological and physiological evidence for aging (Craig 1985) but there have been few studies on changes in the allocation of energy for anabolic and catabolic processes. Orton's theory (Orton 1929) that over-production can lead to death states that the allocation of energy for reproduction increases with age at the expense of the soma. The balance between reproductive output and somatic maintenance has been summarized by Calow (1985). The way energy is partitioned between metabolic demands is likely to have a profound effect on time to and between breeding events, survivorship, and fecundity of the adult fish. Biological organisation is continuously being impaired; to remain viable the impaired structures must be replaced or repaired. For example, the energy for protein synthesis makes up about 25% of the fasting metabolic rate (Waterlow 1980). Alternatively reproductive investment may be at the expense of these maintenance processes.

The basic biology of goldeye, *Hiodon alosoides*, was recorded by Kennedy and Sprules (1967) but little has been published on their ecology. They are almost unique among freshwater fish species in producing a semi-buoyant egg. Also the amount of milt produced by the male is very small and indicates that the male must be in very close proximity to the female during spawning. However, the spawning act has not been observed since it takes place in turbid waters (Scott and Crossman 1973). Spawning occurs soon after the break up of ice and gonadal recrudescence starts immediately after spawning. It is complete by the end of the open water season (Pankhurst 1985; Pankhurst et al. 1986). This development of the gonad is unlike that in the majority of temperate freshwater fish which store energy in the soma and then gradually transfer it to the gonads (Craig 1977). As a result the allocation of energy intake to the various body tissues and organs in the goldeye is easier to measure. Other studies on perch, *Perca fluviatilus* (Craig 1977), and Baltic cod, *Gadus callarias* (Bogoyavlenskaya and Vel'tishcheva 1972), appear to provide support for Orton's theory. The present study was designed to directly test this theory.

Methods

Collection

Goldeye were collected by multi-mesh gillnets from the Battle River, Alberta, from July to November, 1983. Since it

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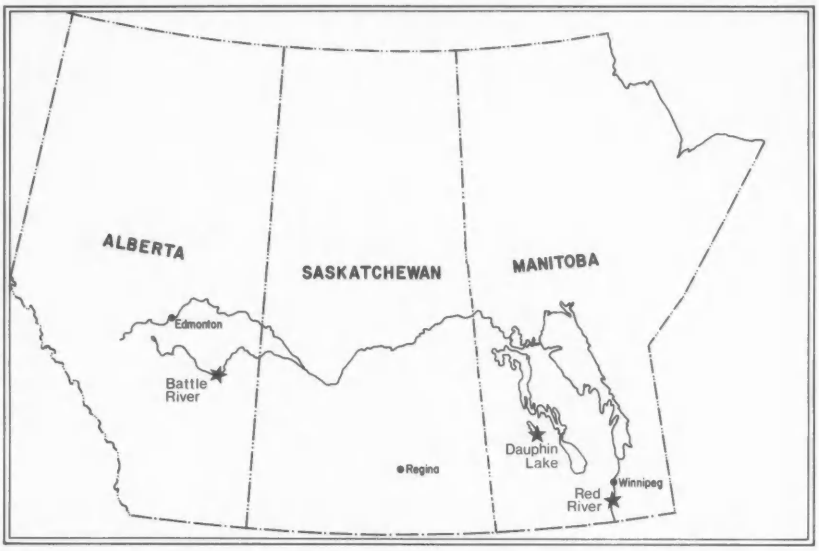

FIG. 1. Map showing the sites used for goldeye collections.

was not possible to collect prespawning fish in the spring from the Battle River, additional samples were taken from Dauphin Lake, Manitoba, in May 1984 and 1985 (Fig. 1). Samples for comparison with the Battle River goldeye were collected from Dauphin Lake in July, September, and November 1984 and 1985. Further samples were gathered from the Red River, Manitoba, in January, March, April, and May during 1984 and 1985 for growth measurements. Goldeye in the Battle River undergo very little exploitation while those in Dauphin Lake (light commercial) and particularly those in the Red River (heavy angling) are exploited. Fish age was determined by counting bands on opercula. These bands appear on the bones mainly in June (J. F. Craig, unpubl. data) and were used to back-calculate growth. After weighing (to nearest gram) and measuring the fish (fork length in millimetres), the goldeye were dissected and divided into muscle fillets, liver, gonad, gut (minus its contents), and carcase (composed of the remaining tissues and organs). These items were weighed to the nearest 0.001 g except the carcase which was weighed to the nearest 0.1 g.

A separate sample of female fish was collected during September, October, and November 1983 from the Battle River. The eggs of these fish were stored in Gilson's fluid. The eggs were later counted for fecundity estimates.

Body Composition

The proximate composition of tissues was determined, mainly from the Battle River fish. Water content was measured by freeze-drying (mean −57°C, range −50 to −60°C). Drying was continued until constant weights were achieved. Lipid determinations were based on a modified Bligh and Dyer method using chloroform and methanol (Hanson and Olley 1963; Craig 1977). A muffle furnace set at 600°C was used to estimate ash content. Ash content of the testes was not determined owing to small sample size. Total nitrogen was measured by the Kjeldahl method (AOAC 1960). Protein content was estimated by assuming that 16% of the nitrogen was nonprotein and multiplying the remaining protein nitrogen by a factor of 6.25 (Craig 1977). The protein content of testes and livers of the males was not determined.

TABLE 1. Values for the statistics of the Von Bertalanffy equation, age at which 95% of the growth is complete ($A_{.95}$, yr) oldest age of fish caught (yr) and first age of maturity (yr) for female and male goldeye from the Battle River (BR), Dauphin Lake (DL), and the Red River (RR).

	Female			Male		
	BR	DL	RR	BR	DL	RR
L_∞	375	355	318	346	327	292
K	0.28	0.29	0.33	0.32	0.35	0.47
t_0	−0.39	−0.30	−0.39	−0.25	−0.20	−0.11
$A_{.95}$	10	10	9	9	8	6
Oldest caught	16	10	8	14	12	6
First age of maturity	5	5	4	4	4	3

The energy values of extracted lipids obtained by pooling samples from Dauphin Lake over the whole study period for the various tissues and organs were estimated by calorimetry using a Parr macrobomb calorimeter. An analysis using phenol and sulphuric acid (Montgomery 1957) was carried out to determine the glycogen content of some of the livers.

The fatty acid composition of tissues and organs was determined by the following procedure (M. Yurkowski, pers. comm.). Lipids were obtained as for energy content determinations. The lipids were transesterified by heating for 90 min at 70°C in 5% methanolic HCl. The fatty acid methyl esters were purified (silica gel H thin-layer plates, 25 mm thick; toluene solvent). Fatty acids were analysed by capillary gas chromatography (Varian Aerograph chromatograph, model 2100, modified for capillary columns; Supelcowax 10 glass columns, 60 m × 0.75 mm outside diameter). The injector and detector temperatures were 250°C and the oven temperature was 193°C. Peak areas were measured and converted to weight percent by a computing integrator (Shimadzu Chromatopac, model C-

TABLE 2. (i) Values of regression coefficient (b) and intercept (a) for log weight (grams) of body organ on log length (millimetres) for male and female goldeye. The correlation coefficient (r) is given plus statistics from which 95% CL can be estimated. (ii) Weights of body organs of a goldeye of fork length of 327 mm from the Battle River. Percentages are given in brackets. The carcase weights of Dauphin Lake (DL) fish are also presented.

(i)

Male	Muscle	Liver	Testes*	Gut	Carcase
b	2.692	3.247	3.932	2.837	2.677
r	0.897	0.868	0.742	0.891	0.953
S^2	0.021	0.042	0.159	0.025	0.009
$\Sigma(x-\bar{x})^2$	0.655	0.655	0.353	0.655	0.655
N	62	62	33	62	62
df	54	54	28	54	54
$a_{combined}$	−10.749	−17.253	−21.436		
a_{BR}				−12.959	−9.883
a_{DL}				−13.533	−10.187
Female					
b	2.575	4.275	4.126	2.864	2.683
r	0.786	0.824	0.769	0.818	0.956
S^2	0.031	0.666	0.085	0.031	0.005
$\Sigma(x-\bar{x})^2$	0.490	0.493	0.550	0.493	0.491
n	72	73	84	72	72
df	64	65	76	64	64
$a_{combined}$	−10.040	−23.122		−13.446	
		a_{July}	−21.529	a_{BR}	−9.868
		$a_{Aug.-May}$	−20.233	a_{DL}	−10.191

(ii)

	Female wt (g) (%)		Male wt (g) (%)
Muscle	130.0 (26.8)		126.4 (28.6)
Liver	5.1 (1.0)		4.7 (1.1)
Ovaries/testes			
Aug.–May	38.7 (8.0)	Sept.–May	3.8 (0.9)
Gut	23.0 (4.7)		32.0 (7.2)
Carcase	288.3 (59.7)		274.7 (62.2)
$Carcase_{DL}$	208.7		202.7

*September, October, November, and May only.

R3A, Kyoto, Japan). Individual fatty acids were identified by use of standard fatty acids, by plots of log relative retention times versus chain lengths and by comparison of equivalent chain lengths as described by Jamieson (1975).

Results

Growth

The growth data fitted the Von Bertalanffy growth model (Von Bertalanffy 1938) very well. There were significant differences in growth between sexes from the same water body and between the same sexes from different water bodies (Hotelling's $T^2 = p < 0.001$; Bernard 1981) (Table 1). The oldest fish were obtained from the Battle River. Females in this river grew to a greater ultimate length but at a slower rate than females at the other sites. Males grew to a smaller ultimate length than the females but generally grew faster towards their asymptote.

Length–Weight Relationships

Regression analysis was carried out on ln fish length (L) and ln tissue weight (W). There was considerable variation between fish from the same month, area (Battle River and Dauphin Lake), and sex. Tests of covariance were performed on these analyses between months and areas. Where there were no significant differences between slopes or intercepts data were combined. The results are summarised in Table 2. Also given in the table are weights of the various tissues for each sex for a standard fork length of 327 mm (the average size of female caught) for fish from the Battle River. Tests of significance between slopes of each sex indicated that only the liver was significant ($p < 0.05$). The carcase weights of both the male and female goldeye from the Battle River were significantly heavier than those from Dauphin Lake. The gut weight of males from the Battle River was nearly twice that of males from Dauphin Lake. The mature ovary represents 8.0–9.5% (Battle River and Dauphin Lake females, respectively) of the total body weight compared with the mature testes of 0.9–1.1% body weight. Fecundity was estimated from the following relationship: log Fecundity = −3.4672 − 3.0202 log Length ($p < 0.001$). A 327-mm female was estimated to contain 13 400 eggs.

Water–Fat Relationships

As found in a number of studies (see Love 1970) of different fish, percent fat is highly negatively correlated with percent water in the various body tissues. This is also evident in goldeye (Table 3). Apart from muscle and gut the slopes are significantly different from −1. This indicates that some modification in the proportion of the other components (mainly water and protein) takes place as fat is accumulated (Iles and Wood 1965).

Body Constituents and Age

Regressions were calculated for each organ or tissue for ln weight of proximate component on age (Table 4). The slopes of these regressions give estimates of instantaneous rates of growth (gram per gram per year). In most cases the relationships were highly significant ($p < 0.001$). The regression for fat of the gut were nonsignificant. This was due to high variability between individuals. Fat values for the gut were recalculated from data on water composition (Table 3). In males, testes exhibited considerable variations in weight between individuals for any month and no statistically significant relationships could be determined. The growth rate of males, in general, tended to be higher than that of females. The water content of tissues increased at or slightly above the rate of increase of the whole organ except in the case of the gut in which the rate of water increase was significantly higher (Table 5). In consequence the rate of increase in fat of the gut was much lower than that of the weight of the gut as a whole. The rate of increase of fat of the ovary was much higher than that of the whole organ. The energy values of lipids extracted from organs were highest for the ovary and lowest for the gut (Table 6). The value given for the soma (whole body of the fish minus the gonad) in the table is based on a standard fish of length 327 mm.

The relative percentage weights of the fatty acids of the lipids extracted from the various body organs and tissues are listed in Tables 7 and 8. Gut, muscle, and carcase had a similar fatty acid complement which may have reflected the composition of the goldeye diet. The liver would appear to have selected or synthesized certain fatty acids which were utilised by the developing ovary or testes. The ovary in comparison to gut, muscle, and carcase was low in saturated fats but high in the essential fatty acids (n6 and n3). The testes selected saturated fats.

TABLE 3. Values of pooled regression coefficient (b) and intercept (a) for percent fat on percent water for body organs of goldeye. The correlation coefficient (r) is given plus statistics from which 95% CL can be estimated. The significance of b from -1 is presented. NS = nonsignificant.

	Muscle	Liver	Ovaries	Testes	Gut	Carcase
b	−0.981	−0.212	−0.563	−0.526	−1.001	−0.842
r	−0.919	−0.455	−0.577	−0.677	−0.953	−0.889
S^2	1.479	2.163	35.013	0.634	12.380	2.559
$\Sigma(x-\bar{x})^2$	926.131	618.515	3033.901	19.400	13207.246	1506.360
n	116	54	58	12	112	116
df	111	49	55	10	107	111
a	80.865	22.868	60.068	45.618	88.949	67.240
Significant from −1	NS	<0.001	<0.001	<0.05	NS	<0.001

TABLE 4. Regression equations describing relationships between age (x) and ln proximate composition weight of the tissues and organs of female and male goldeye. The significance of the regression is also given where * = $p<0.05$, ** = $p<0.01$, and *** = $p<0.001$.

Organ or tissue	Total	Water	Ash	Fat	Protein
Female					
Muscle	$4.332+0.071x^{***}$	$3.994+0.073x^{***}$	$-0.058+0.057x^{***}$	$2.116+0.055x^{*}$	$2.476+0.064x^{***}$
Liver	$0.807+0.129x^{***}$	$0.518+0.130x^{***}$	$-3.057+0.083x^{**}$	$-1.052+0.079x^{*}$	$-0.799+0.092x^{**}$
Gut	$2.421+0.104x^{***}$	$1.683+0.135x^{***}$	$-3.029+0.118x^{***}$	$1.574+0.052x^{a}$	$-0.343+0.130x^{***}$
Carcase	$4.801+0.109x^{***}$	$4.237+0.117x^{***}$	$1.693+0.135x^{***}$	$3.256+0.078x^{***}$	$2.927+0.104x^{***}$
Ovaries	$2.780+0.092x^{***}$	$2.093+0.098x^{***}$	$-1.579+0.061x^{*}$	$1.249+0.133x^{***}$	$1.435+0.080x^{*}$
Soma	$5.404+0.098x^{***}$	$4.875+0.105x^{***}$	$1.874+0.128x^{***}$	$3.725+0.067x^{***}$	$3.491+0.092x^{***}$
Male					
Muscle	$4.051+0.081x^{***}$	$3.605+0.104x^{***}$	$-0.486+0.098x^{***}$	$1.421+0.096x^{*}$	$2.111+0.098x^{***}$
Liver	$0.378+0.138x^{***}$	$0.062+0.138x^{***}$	$-4.015+0.147x^{***}$	$-2.218+0.137x^{a}$	—
Gut	$2.480+0.103x^{***}$	$1.453+0.145x^{***}$	$1.015+0.015x^{***}$	$1.889+0.060x^{a}$	$-0.281+0.119x^{***}$
Carcase	$4.450+0.134x^{***}$	$3.900+0.144x^{***}$	$1.417+0.158x^{***}$	$2.928+0.085x^{***}$	$2.587+0.129x^{***}$
Soma	$5.115+0.117x^{***}$	$4.575+0.122x^{***}$	$1.701+0.136x^{***}$	$3.551+0.061x^{**}$	$3.249+0.100x^{***}$

[a]Based on estimated fat values from percent water (Table 3).

TABLE 5. Ratios of the regression coefficients slopes from Table 4 of each component of the tissue or organ to the total coefficient value. The coefficients may be considered as instantaneous growth rates (gram per gram per year).

	Water	Ash	Fat	Protein
Female				
Muscle	1.02	0.80	0.77	0.90
Liver	1.01	0.64	0.61	0.71
Gut	1.30	1.13	0.50	1.25
Carcase	1.07	1.24	0.72	0.95
Ovaries	1.06	0.66	1.45	0.87
Soma	1.07	1.31	0.68	0.94
Male				
Muscle	1.28	1.21	1.18	1.21
Liver	1.00	1.06	0.99	—
Gut	1.41	0.15	0.58	1.15
Carcase	1.07	1.18	0.63	0.96
Soma	1.04	1.16	0.52	0.85

TABLE 6. Energy values of lipid extracts of goldeye with percent error betwen replicates. The value given for the soma is based on the weights of 327-mm fish. Values of the soma for other organisms are given for comparison.

Organ	Energy value (Kcal·g^{-1})	Percent error
Ovaries	9.59	0.1
Muscle	8.61	0.5
Liver	8.55	0.8
Testes	8.09	1.6
Carcase	8.00	1.5
Gut	7.40	0.1
Soma		
Goldeye	8.11	
Perch (*Perca fluviatilis*)	8.49 Craig (1977)	
Largemouth bass (*Micropterus salmoides*)	8.5 Beamish et al. (1975)	
Mammal	9.45	

The glycogen content of the liver varied extensively even between fish caught at the same time and in the same place, of the same sex and maturity. Values ranged from 0.36 to 49.10 mg·g^{-1}. The differences can probably be accounted for by the length of time the fish were held in the nets and are an indicator of chronic stress (Love 1980; Wedemeyer and McLeay 1981). Glycogen estimates are only relevant in energetic studies when fish are held under controlled laboratory conditions.

Discussion

The linear relationship between the statistic K (from the Von Bertalanffy equation) and instantaneous mortality (M) is well established for a number of fish stocks (Pauly 1980). As the rate (K) at which fish grow towards their maximum size (L_∞) increases so does the instantaneous mortality rate of the pop-

TABLE 7. Relative composition (percent) of the main fatty acids in goldeye organs and tissues.

	Tissue/organ					
Fatty acid	Ovary	Testes	Liver	Gut	Muscle	Carcase
14:0	0.48	2.06	1.11	2.57	1.83	3.03
16:0	4.95	21.37	16.80	17.06	17.59	13.86
16:1n9	1.35	0.13	0.06	0.10	0.12	0.13
16:1n7	19.36	14.65	8.98	16.13	15.59	14.21
18:0	1.33	7.44	9.43	3.64	3.38	4.00
18:1n9	34.10	28.68	19.63	32.81	32.67	33.71
18:1n7	5.76	7.65	6.88	6.79	6.28	6.50
18:2n6	5.81	1.81	2.55	3.23	3.39	4.21
18:3n3	5.80	1.14	1.82	2.52	2.45	3.16
20:4n6	1.93	0.55	5.73	1.11	0.92	1.05
20:5n3	2.85	0.57	5.80	1.47	1.46	1.79
22:4n6	0.26	0.26	0.46	0.19	0.13	0.14
22:5n6	0.16	Trace	0.31	0.08	—	0.09
22:5n3	1.31	0.25	1.92	0.71	0.72	0.77
22:6n3	4.11	0.51	7.12	0.95	0.32	1.17

ulation increase. Thus faster growth induces earlier senescence. The differences in *K* and the oldest goldeye caught between sexes and areas would support this relationship. Red River goldeye, compared with other populations, show a typical response to heavy exploitation: faster growth, earlier maturity, and curtailed life span. The Battle River goldeye were considered to be the most appropriate population in which to investigate changes in body composition with age since they were unexploited. During the open water period anabolic energy is allocated to development of the gonad. Ingested energy is also stored for maintenance metabolism during the winter. The ovary is fully developed by August and it does not differ significantly in weight from that of the prespawning condition in May.

As expected, from the study of a natural population, there was considerable variation in the composition of the various body organs between individuals probably due to different rates of feeding and energy accumulation during the summer months. However in most cases it was possible to relate weight of tissue component to age of the fish. Fat can be considered to be the chief form of stored energy in fish (Shul'man 1974). The proportion of fat to the total in the muscle, liver, gut, and carcase of female goldeye and gut and carcase of male goldeye declined with age while that of the ovary increased. The ovary enlarges at the expense of the soma. The decline in fat of the soma is progressive as the fish gets older. By implication more energy is needed for the ovaries of older fish. The ovary appears to select certain fatty acids particularly essential fatty acids, n6 and n3. These have been shown to be important in embryonic development in a number of freshwater fish species (Henderson and Tocher 1987). The syntheses or selection of these fatty acids is undertaken by the liver. The rate of fat accumulation in the gut was lower than in other organs. Thus it appears that allocation of fat to the gonad was particularly at the expense of fat accumulation by the gut. The proportion of protein in the body tissues and organs of both sexes remained approximately constant with age. Ash content increased in the carcase of older female and male fish.

When the energy value of the soma and gonad of female goldeye from the Battle River were calculated, from conversion factors of 5.65 $Kcal \cdot g^{-1}$ for protein and those given in Table 6 for lipid, the energy content of the soma increased by 44% and that of the ovary by 121% between the ages of 10–16 yr. Orton's theory cannot be supported merely because the energy content of the soma increases at a slower rate than that of the gonad. This is a necessary but not sufficient requirement to support Orton's point that the gonad increases at the expense of the soma. To demonstrate this it should be clear that the soma energy content could and would increase at a faster rate if the gonad were not there. Perhaps a comparison with the male would help to prove this point. In the male, gonad growth is minimal (nonmeasurable) compared with the female and possibly as a result the male soma grows faster than the female. One confounding factor may be differences in energy intake to compensate for the greater energy demand of the ovary as demonstrated for northern pike, *Esox lucius* (Diana 1983). Orton's theory seems to be well supported by these findings. Fish of all ages showed signs of gonadal development from August to May and there was no indication of a postreproductive phase in old fish. Thus it would appear that goldeye channelled energy into reproduction at the expense of the soma.

TABLE 8. Summary of the fatty acid composition of goldeye tissues and organs.

	Tissue/organ					
Fatty acid	Ovary	Testes	Liver	Gut	Muscle	Carcase
saturated (14:0,15:0,16:0,17:0,18:0, 20:0,22:0)	7.10	31.82	28.52	24.46	24.00	22.42
n9 (16:1n9,18:1n9,20:1n9)	35.79	29.89	20.11	33.33	33.23	34.41
n7 (16:1n7,18:1n7,20:1n7)	25.33	22.46	16.04	23.00	21.94	20.82
n5 (16:1n5,18:1n5)	0.68	0.78	0.80	0.85	0.85	0.85
n6 (18:2n6,20:4n6,22:4n6,22:5n6)	8.16	2.62	9.05	4.61	4.44	5.49
n3 (18:3n3,20:3n3,20:4n3,20:5n3, 22:5n3,22:6n3)	15.16	2.71	17.31	6.16	5.47	7.50

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Mechanisms of Tri-N-Butyltin Bioaccumulation by Marine Phytoplankton[1]

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We examined uptake of tri-n-butyltin (TBT) by three genera of marine microalgae and one genus of cyanobacterium. There was a linear relationship between external concentrations of TBT and cell burdens in the microalgae *Nannochloris* sp., *Chaetoceros gracilis*, and the cyanobacterium *Synechococcus* sp. (PR-6). The relationship between external TBT concentrations and cell TBT burdens was distinctly nonlinear for *Isochrysis galbana*. Competitive binding experiments showed a decrease of approximately 88% of the total bound radiolabeled TBT to *I. galbana* in the presence of a 200-fold excess of unlabeled TBT. No significant decrease of bound TBT was observed for *Nannochloris* sp. These studies demonstrate that either partitioning or binding may control bioaccumulation of TBT by marine phytoplankton.

Nous avons étudié l'absorption du tri-n-butylétain (TBT) par trois genres de micro-algues marines et par un genre de cyanobactérie. On a observé une relation linéaire entre les concentrations externes de TBT et les charges cellulaires dans les micro-algues *Nannochloris* sp., *Chaetoceros gracilis*, et chez la cyanobactérie *Synechococcus* sp. (PR-6). On n'a pu établir de relation linéaire entre les concentrations externes de TBT et les charges cellulaires en ce composé dans le cas de *Isochrysis galbana*. Des expériences de liaison compétitive ont mis en évidence une diminution d'environ 88% du TBT total lié et radiomarqué pour *I. galbana* en présence d'une quantité de TBT non marqué 200 fois supérieure. On a observé aucune diminution significative du TBT marqué chez *Nannochloris* sp. Ces études ont permis de démontrer que le partage ou la liaison pouvaient exercer un certain contrôle sur la bioaccumulation du tri-n-butylétain par le phytoplancton marin.

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Recently, tributyltin compounds (TBT) have been used as biocides, particularly in marine antifouling coatings (Evans and Smith 1975). A major problem with their use as antifouling agents is leaching of these compounds into surrounding waters, which causes toxicity to nontarget marine organisms, and in some cases, to economically important species. Studies of TBT bioaccumulation have tended to focus on molluscs and fish consumed by man (Waldock and Thain 1983; Short and Thrower 1986; Davies et al. 1986). In the environment, microorganisms dominate on the basis of biomass; some form the basis of many marine food chains. If TBT accumulation through food chains is important, microorganisms such as phytoplankton will play a significant role.

The mechanisms responsible for bioaccumulation have received much less attention than toxicity, environmental flux and compartmentalization. For example, the effects of organotin compounds on cyanobacterium and marine microalgae have been well documented. These include reduced growth rates (Beaumount and Newman 1986), inhibition of phosphorylation in chloroplasts (Millner and Evans 1981) and even cell death (Beaumount and Newman 1986). Many reports have demonstrated the binding and accumulation of organometallic compounds to microorganisms (Silverberg et al. 1976), yet little is known about the mechanism by which marine phytoplankton accumulate organotins. Blair et al. (1982) reported that bacteria isolated from the Chesapeake Bay area (*Pseudomonas* strain 244) rapidly bound TBT via an energy-independent mechanism. Maguire et al. (1984) showed that the green alga, *Ankistrodesmus falcatus* accumulated TBT over a 4-wk period resulting in bioconcentration levels of 3×10^4. This level is far in excess of one that can be explained by simple partitioning (Laughlin et al. 1986). The studies reported here had two major objectives: first, to compare the extent of TBT uptake for three marine microalgae species and one cyanobacterium species; second, to determine mechanisms responsible for TBT uptake.

Materials and Methods

Cell Culture

Microalgal isolates were obtained from Harbor Branch Oceanographic Institution culture collections. Marine microalgae used were *Isochrysis* aff. *galbana* (Tahitian isolate), *Nannochloris* sp., and *Chaetoceros gracilis*. The cyanobacterium was *Synechococcus* sp. (PR-6). In all cases cultures were unialgal but not necessarily axenic. Eukaryotes were grown in 32 salinity F/2 medium (Guillard and Ryther 1962). The cyanobacterium was cultured in 28 salinity ASP II medium (Provalsoli et al. 1957). Phytoplankton were maintained in 2-L Erlenmeyer flasks and harvested for these studies during log phase growth. All cultures were placed into

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an environmental chamber maintained at 24°C (± 2) with a 16:8 h light–dark cycle. *Synechococcus* sp. (PR-6) was grown at 35°C in continuous light as described by Myers (1950).

Tri-n-butyltin Accumulation Assay

Seawater used in these experiments was filtered (0.45-μm nitrocellulose filter, Millipore) estuarine seawater (30–35 salinity) obtained from the Indian River Lagoon (Florida, USA). Stock solutions of unlabeled TBT (Alfa Products), and radiolabeled TBT ([butyl-1-^{14}C] Bis[tri-n-butyltin]) oxide (New England Nuclear, 138 MBq·mmol^{-1}) were prepared in absolute alcohol as the solvent carrier. Typically, 11 exposure concentrations of TBT were tested ranging from 20 ng·L^{-1} to 2 mg·L^{-1}. The highest concentration is approximately the solubility of TBT in seawater. Accumulation experiments were conducted in acid-washed (3.2 M nitric acid, 18 h) polycarbonate centrifugation tubes. Solution volumes for TBT concentrations of 2 mg·L^{-1} to 1 μg·L^{-1} were 50 mL. Due to the low relative specific activity of the radiolabeled TBT, 250-mL volumes were employed for concentrations below 1 μg·L^{-1}. Cell densities during experiments were 1.5×10^5 cells·mL^{-1} and 1.0×10^6 cells·mL^{-1} for the microalgae and cyanobacterium, respectively.

Accumulation tests were initiated by adding the microorganisms directly to polycarbonate bottles containing seawater and the indicated concentrations of TBT. After 2 h at 25°C, cells were collected by centrifugation (10 000 g for 10 min at 4°C). The supernatant was decanted and the cell pellet rinsed with 5 mL of seawater. Cells were then resuspended with 0.2 mL of seawater and digested for 2 h (25°C) by adding 0.2 mL Soluene 350 tissue solubilizer (Packard). Approximately 10 mL ASC liquid scintillation cocktail (Amersham/Searle) and 0.2 mL acetic acid were added to the vials containing cell digests. Acetic acid was added to minimize chemiluminescence. The amount of radiolabeled TBT was then determined by liquid scintillation spectrophotometry. Initially, accumulation of TBT by marine phytoplankton was monitored by exposing microorganisms to concentrations of [^{14}C]-TBT ranging from 20 ng·L^{-1} to 2 mg·L^{-1}; however, we were unable to measure bound TBT reproducibly at concentrations below 1 μg·L^{-1}, probably due to small cell volume in each sample. Accumulation of TBT was easily measured with concentrations ranging from 1 μg·L^{-1} to 2 mg·L^{-1}.

Competition Experiments

A series of TBT solutions were prepared so that microorganisms were exposed to identical concentrations of radiolabeled TBT (nominally 5 μg·L^{-1} in 50 mL). The final concentration of TBT was achieved by adding the indicated amount of unlabeled TBT. Because of the low specific activity of the radiolabeled TBT, cell densities in these experiments were increased to 3×10^5 cells·mL^{-1}. Following exposure for 1 h at 25°C, the amount of radiolabeled TBT bound to the cells was determined as described above. TBT concentrations in stock solutions were verified using chemical analysis based on hydride derivatization with atomic absorption detection (Valkirs et al. 1985). Statistical analysis of the data were performed using the Statistical Analysis System Institute (Raleigh, NC, USA, software package SAS-PC). Each point in Figures represent the mean and standard deviations of at least three independent determinations.

Results

Uptake of TBT by *Chaetoceros gracilis* or *Nannochloris* sp. was essentially linear at 1 μg·L^{-1} to 2 mg·L^{-1} (Fig. 1a,b). Correlation coefficients (r^2) were 0.993 and 0.974 for *Nannochloris* sp. and *C. gracilis*, respectively. The pattern of TBT uptake by *Nannochloris* sp. was similar to that for *C. gracilis*, but quantitatively, *C. gracilis* accumulated substantially greater amounts of TBT (Fig. 1b). Linear relationships between external concentrations and cell burdens of a hydrophobic compound implies partitioning as the mediating mechanism for uptake.

The pattern of TBT uptake by *Isochrysis galbana* (Fig. 1c) was different from both *C. gracilis* and *Nannochloris* sp. The relationship between external concentration and cell burdens was distinctly nonlinear and appeared to saturate at concentrations of TBT in excess of 1 mg·L^{-1}. In contrast to the data obtained for *C. gracilis* and *Nannochloris* sp., we could measure the accumulation of TBT by *I. galbana* at concentrations as low as 20 ng·L^{-1}. These data suggest that a large component of accumulation by *I. galbana* is due to a specific saturable interaction of TBT with cell surface components. From a quantitative aspect, *I. galbana* and *Nannochloris* sp. had cell burdens of only 1/20 and 1/7, respectively in relation to *C. gracilis*.

Accumulation of TBT by the marine cyanobacterium *Synechococcus* sp. (PR-6) was linear ($r^2 = 0.907$) within the concentrations of TBT from 20 μg·L^{-1} to 2 mg·L^{-1}, but below 20 μg·L^{-1} the measurable uptake was not consistent (Fig. 1d). Interestingly, *Synechococcus* sp. (PR-6) had the lowest accumulation of TBT per cell density of all of the marine microorganisms tested.

To characterize further the mechanism of TBT uptake, competitive binding assays were performed using *I. galbana* and *Nannochloris* sp. These experiments were designed to monitor the effects of increasing concentrations of unlabeled TBT on a fixed amount of bound radiolabeled TBT. If partitioning is the dominant mode of accumulation, then the concentration of [^{14}C]-TBT associated with the cells will be independent of the unlabeled TBT concentration in solution. On the other hand, if a component of the accumulation is mediated by a specific saturable process, then the amount of [^{14}C]-TBT associated with the cells will decrease as the concentration of unlabeled TBT in solution increases.

Unlabeled TBT in solution decreased the amount of bound radiolabeled TBT to *I. galbana* (Fig. 2). The decrease was dependent on the concentration of unlabeled TBT in solution; approximately 37 and 12% of the total [^{14}C]-TBT remaining bound in the presence of 100 and 1000 μg·L^{-1} TBT, respectively. On the other hand, we observed only a 26% decrease in the total amount of accumulated TBT by *Nannochloris sp.*, regardless of the total external TBT concentration. In fact, differences between mean counts bound at any concentration of unlabeled TBT were not statistically significant ($F = 0.64$; $p = 0.44$). These results in conjunction with the data presented in Fig. 1c, suggest that TBT interacts with *I. galbana* in a specific saturable manner, whereas accumulation by *Nannochloris* sp. is due largely to partitioning. Interestingly, concentrations of unlabeled TBT as high as 500 μg·L^{-1} were ineffective at decreasing the total amount of labeled TBT bound to *Synechococcus* sp. (PR-6) (data not shown). These results and the data represented in Fig. 1d suggests partitioning as a mode for accumulation.

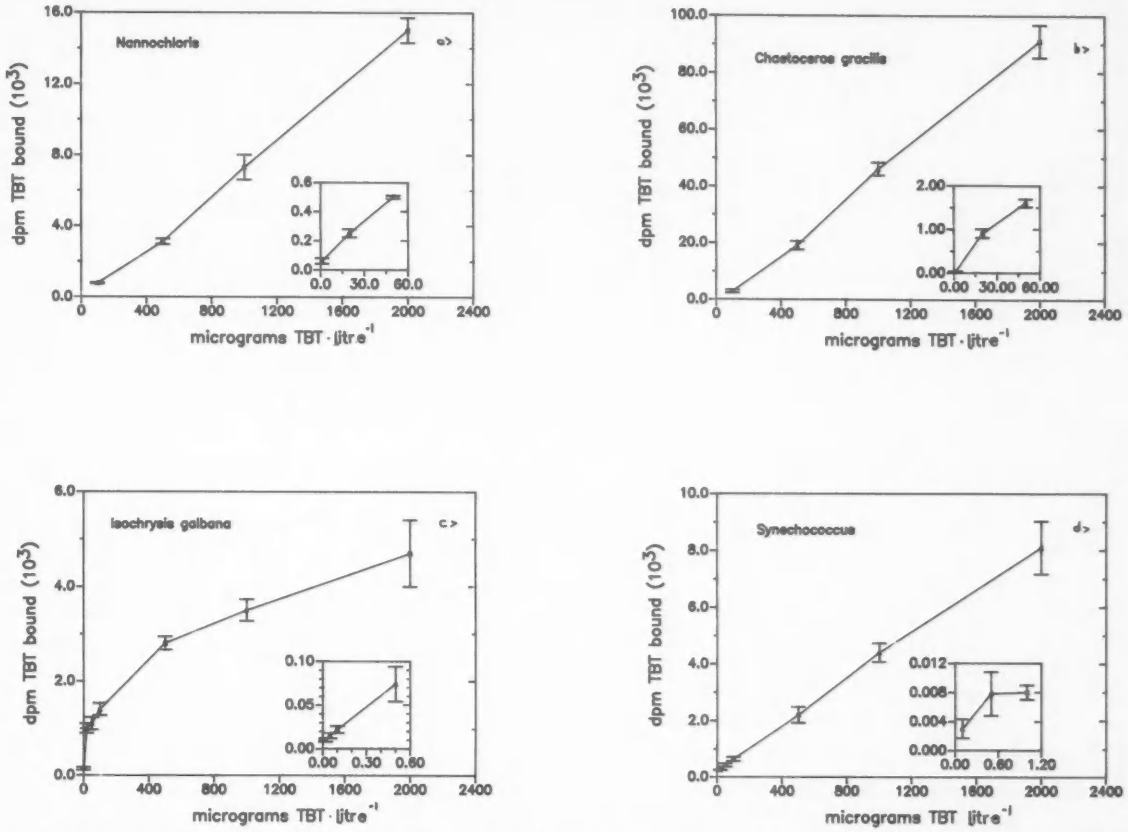

FIG. 1. Accumulation of [^{14}C]-TBT by (a) *Nannochloris* sp.; (b) *Chaetoceros gracilis*; (c) *Isochrysis galbana*; (d) *Synechococcus* sp. (PR-6). Cells were incubated for 2 h with the indicated concentrations of TBT. Inset shows expanded axis scales for data obtained at concentrations of TBT below 60 $\mu g \cdot L^{-1}$ (a,b), 0.6 $\mu g \cdot L^{-1}$ (c), and 1.2 $\mu g \cdot L^{-1}$ (d).

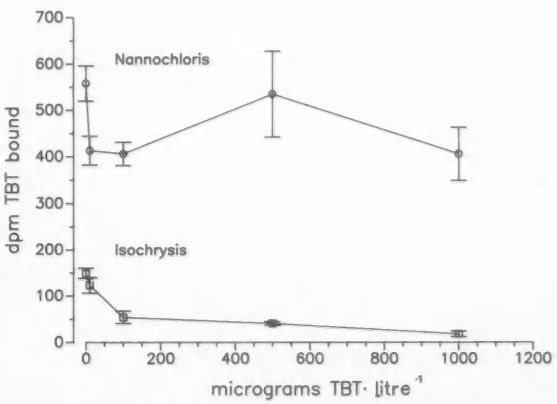

FIG. 2. Competitive binding of TBT by marine microalgae. Approximately 5 $\mu g \cdot L^{-1}$ of [^{14}C]-TBT was incubated with cells (1 h) in the absence or presence of 10, 100, 500, and 1000 $\mu g \cdot L^{-1}$ unlabeled TBT.

Discussion

Our results clearly demonstrate that all four genera of marine phytoplankton accumulate TBT. The linearity of the relationship between exposure concentrations and cell burdens for *Nannochloris* sp., *Chaetoceros gracilis*, and *Synechococcus* sp. (PR-6) suggests that TBT is being accumulated by these cells via hydrophobic partitioning. This mode of uptake is considerably enhanced due to the three alkyl moieties covalently bonded to the tin atom. In fact, the alkyl groups influence the physical and chemical characteristics of TBT. Lipophilicity, as measured by n-octanol water partition coefficient, is thought to be the dominant parameter for bioaccumulation (Leo 1975) as well as toxicity (Schultz et al. 1980; Wong et al. 1982). For example, differential accumulation of TBT in tissues correlates well with lipid content (Laughlin et al. 1986) and the order of toxicity for microalgae and terrestrial animals is also dependent on the organic moieties (i.e. trialkyl > dialkyl > monoalkyl; Wong et al. 1982; Zuckerman et al. 1978).

The pattern of binding of TBT to *Isochrysis galbana* suggested a specific saturable binding mechanism. If [^{14}C]-TBT was nonspecifically saturating the lipid reservoir, addition of unlabeled TBT would not displace the [^{14}C]-TBT. We observed that addition of unlabeled TBT (1 $mg \cdot mL^{-1}$) actually decreased the amount of bound [^{14}C]-TBT by approximately 88%. This pattern is compelling evidence for a specific interaction with membrane components which contain receptor sites. The nature of this membrane component is unclear at present; however, if the TBT cation were involved, a likely candidate could be negatively charged groups such as carboxylic acids of membrane-

bound proteins. The number of active sites appears to be easily saturated, thus limiting the extent of bioaccumulation and cell burdens. Indeed, Maguire et al. (1984) have suggested the involvement of the TBT cation in accumulation and metabolism by green alga. In addition to the different mechanisms for TBT uptake, these studies demonstrate that marine microalgae may also be distinguished by the extent of TBT accumulation.

In conclusion, all phytoplankton species we tested accumulated TBT during experimental exposures of short duration. Partitioning was the mode in three species tested, while saturable binding controlled accumulation in one species. There was a large difference, by a factor of 20, in the cell-specific amount of TBT accumulated by each species. The large difference in accumulation by different species should not obscure the importance of distinguishing mechanisms of accumulation. The species which binds TBT had measurably more TBT at low concentrations typical of many aquatic environments. Thus, species displaying this method of TBT uptake may play a disproportionate role in environmental flux and compartmentalization of TBT.

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Reproductive Success of *Amnicola limosa* (Gastropoda) in Low Alkalinity Lakes in South-Central Ontario

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The reproductive success of the gastropod *Amnicola limosa* was examined in six lakes ranging in pH from 4.62 to 7.42 to determine which stages in the life cycle were most sensitive to acidification. Although fecundity was significantly greater ($p < 0.01$) for adults reared at pH 7.42 than at pH 5.89–6.64, a failure to oviposit was documented only at pH 4.62. Hatching success was uniformly high (88–97%) at pH 5.59 to 7.42, while embryos incubated at pH 4.62 suffered complete mortality. The most critical stage in the life cycle is the newly hatched stage. Survival during the 20 d post hatch ranged from 23% at pH 5.59 to 69% at pH 7.42. There was an order of magnitude difference in the cumulative percent survival of recruits in lakes ranging in pH from 5.59 (5.1%) to 7.42 (44.0%). Juveniles raised at low pH (5.59–5.70) were on average 0.20 mm (20%) smaller than those in circumneutral lakes (pH 6.64–7.42). The present low densities of *Amnicola limosa* in Heney Lake (pH 5.59) can be explained by low recruitment since 1980. Evidence presented suggests that the disappearance of this species from clear low pH lakes (pH <5.8) is due to reductions in fecundity and hatchling survival.

On a étudié la reproduction du gastéropode *Amnicola limosa* dans six lacs de pH allant de 4,62 à 7,42 pour déterminer quels stades du cycle biologique de cette espèce sont les plus sensibles à l'acidification. On a constaté que la fécondité des adultes élevés à un pH de 7,2 était supérieure dans une mesure significative (p inf. à 0,01) à celle des sujets des eaux de pH de 5,89 à 6,64, ce n'est que dans les eaux de pH de 4,62 qu'il n'y a pas eu de ponte. L'éclosion a donné d'aussi bons résultats (88–97%) dans les eaux de pH de 5,59 jusqu'à 7,42, tandis que tous les oeufs incubés à un pH de 4,62 sont morts; juste après l'éclosion commence le stade le plus critique du cycle biologique. Le taux de survie durant les 20 d suivant l'éclosion allait de 23%, au pH de 5,59, à 69%, au pH de 7,42. Le taux de survie cumulatif des recrues différait d'un ordre de grandeur entre les lacs de pH de 5,59 (5,1%) à 7,42 (44%). En moyenne, les juvéniles élevés à faible pH (5,59 à 5,70) mesuraient 0,20 mm (20%) de moins que ceux des eaux au pH proche du point de neutralité (pH de 6,64 à 7,42). Le fait que la population d'*Amnicola limosa* ne soit actuellement pas très dense dans le lac Heney (pH de 5,59) peut s'expliquer par la faiblesse du recrutement depuis 1980. D'après les données présentées, la disparition de ce gastéropode des lacs aux eaux limpides de faible pH (pH inf. à 5,8) est due à la baisse de la fécondité et du taux de survie.

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Despite the wealth of evidence documenting the decline of mollusc populations in acidifying environments (Mackie 1987; Okland and Okland 1986), few reports of the disappearance of individual species have been published. Mossberg (1979) reported the disappearance of the snail *Valvata macrostoma* and several *Pisidium* species from two Swedish lakes when pH's declined to 4.8 and 5.3. More recently, Rooke and Mackie (1984) reported a reproductive failure of *Amnicola limosa* in Heney Lake (pH 5.59) in south-central Ontario in 1980. This species was also found to be extremely rare in another low-pH lake (Plastic Lake, pH 5.70) (Rooke and Mackie 1984). Field experiments conducted by Servos and Mackie (1986) demonstrated that short-term acidification associated with spring melt could not account for the loss of mollusc populations (including *A. limosa*) from acidifying lakes. The reported LC_{50} values for hydrogen ion toxicity for adult and juvenile *A. limosa* are well below the pH depressions commonly reported in acidifying lakes of south-central Ontario (Servos et al. 1985). However, reduced summer growth of adults and juveniles in low alkalinity lakes (Rooke and Mackie 1984; Servos et al. 1985), and the apparent sensitivity of embryonic stages to low pH led Servos et al. (1985) to postulate that recruitment failure and subsequent elimination of *A. limosa* from low-pH lakes may be due to reduced fecundity and/or impaired embryonic development.

Laboratory studies have documented reductions in the reproductive success of juvenile gastropods at low pH. Holcombe et al. (1984) found that adult *Aplexa hypnorum* failed to oviposit, and egg and juvenile survival was significantly reduced when held in water which fluctuated in pH from 3.90–5.65. Significant reductions in growth, fecundity, and hatching success of the pond snail *Helisoma trivolvis* below pH 5.65 have been documented by Garve (1980). Embryos of the cosmopolitan freshwater snail *A. limosa* suffered delayed hatch when held in lake water acidified to pH 5.5, and failed to hatch at or below pH 5.0 (Servos et al. 1985). These results suggest that reproductive failure is a sensitive indicator of pH stress, and may be contributing to the loss of gastropod populations in acidifying environments.

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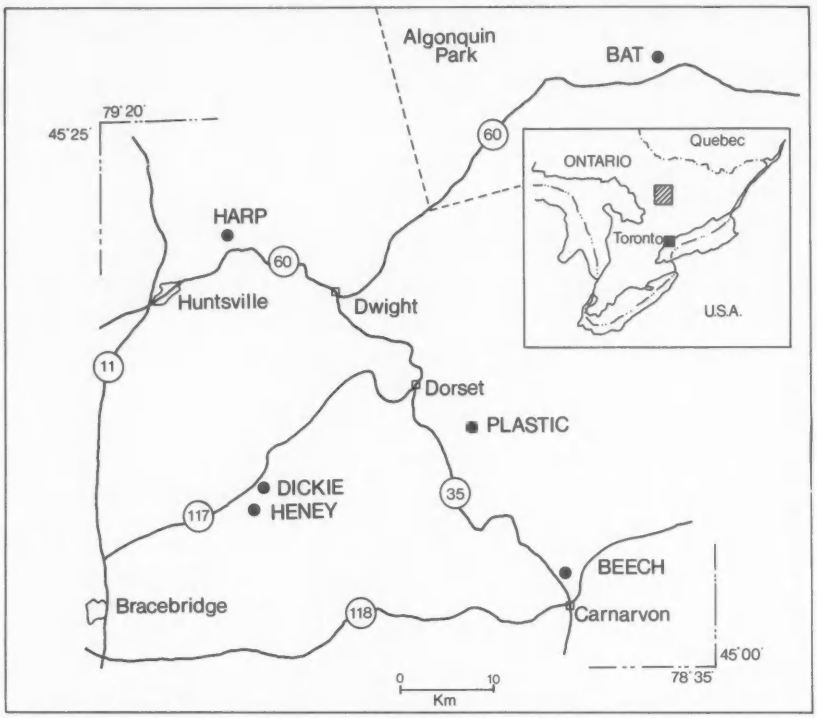

FIG. 1. Map showing the location of the study lakes in south-central Ontario. Highways 11, 35, 60, 117, and 118 are shown in circles.

TABLE 1. Selected water chemistry and lake morphometric data for the six study lakes. All water chemistry values represent average summer epilimnetic concentrations, and are expressed in $mg \cdot L^{-1}$ except where noted. (Data from the Ontario Ministry of the Environment).

	Lake					
Parameter	Bat	Heney	Plastic	Dickie	Harp	Beech
pH	4.62	5.59	5.70	5.89	6.64	7.42
ANC ($\mu eq \cdot L^{-1}$ $CaCO_3$)	−12.0	2.0	1.4	9.4	36.1	151.2
Calcium	0.55	1.97	2.06	2.52	2.94	5.24
Total kjeldahl nitrogen	0.33	0.23	0.16	0.28	0.27	0.26
Total phosphorus ($\mu g \cdot L^{-1}$)	13.3	8.1	6.5	9.9	6.0	6.4
Conductivity ($\mu S \cdot cm^{-1}$)	16	24	22	65	26	60
Colour (Hazen units)	—	10	2	37	23	15
Dissolved organic carbon	3.7	2.8	2.3	4.7	4.4	4.5
$\bar{X}$ depth (m)	4.5	3.3	8.0	5.0	12.4	7.1
Max. depth (m)	8.3	6.5	17.0	12.0	40.0	26.8
Surface area (ha)	3.4	21.7	32.3	93.2	66.9	123.9
Volume ($10^4 m^3$)	15.3	72.4	258.0	464.0	826.0	991.0

The purpose of this study was to document the reproductive success of *A. limosa* in lakes varying in pH and alkalinity to determine which stages in the reproductive process are most affected at low pH. The results of these experiments were combined to compare predicted recruitment of *A. limosa* in a low-pH and a circumneutral environment.

Study Area

The six study lakes had alkalinities <152 $\mu eq \cdot L^{-1}$ ANC (acid neutralizing capacity) and ranged in size from 3.4 to 123.9 ha (Fig. 1). The Muskoka and Haliburton area is underlain almost entirely by Precambrian rock, with an overburden con-

sisting predominantly of till less than 1 m in depth. Although most of the watersheds in the region are poorly buffered, localized areas of carbonate deposits influence watersheds and may account for some of the variation in surface water chemistry (Dillon et al. 1978).

A. limosa was not found in the three most acidic lakes (Bat, pH 4.62, Heney, pH 5.59 and Plastic, pH 5.70), while the remaining lakes (Dickie, pH 5.89, Harp, pH 6.64, and Beech, pH 7.42) supported viable populations. Selected water chemistry and morphometric values for these six lakes are given in Table 1.

Materials and Methods

Transfer of Adults Among Lakes

A field transfer experiment was conducted in May to August 1985 to test whether (i) a failure of females to oviposit or a decline in recruitment following successful egg laying could account for the reproductive failure of *A. limosa* in low alkalinity lakes, and (ii) populations from low, medium, and high pH environments differed in their response to low pH stress. Five lakes were chosen for study, three of which supported *A. limosa* populations; in the other two (Plastic and Heney Lakes), the species had recently been eliminated or was rare (M. A. Shaw, unpubl. data). One hundred and twenty-five mature snails were collected from the littoral zone of three source lakes (Dickie, pH 5.89, Harp, pH 6.64, and Beech, pH 7.42 Lakes). Twenty-five adults from each source lake were transferred to each of five incubation lakes. The set of incubation lakes included the three source lakes, as well as Plastic and Heney Lakes.

All snails were held in cages constructed from 500-ml polyethylene containers with the tops and bottoms replaced with 480-μ nylon mesh. Holes were drilled in the cages to attach them to acrylic strips with nylon nuts and bolts. Conditioned leaf litter (willow leaves removed from the bottom of a pond) was introduced into each cage to provide snails with a source of food. The cages were weighted down with rocks in approximately 0.5 m of water, as close to the outflow of each lake as possible. The outflow was chosen to best represent an integration of the lake water chemistry as a whole (Goldstein et al. 1984).

Snails were collected on May 8–9, 1985, and held at 8°C until transplanted into their respective lakes. Snails to be introduced into the two lowest pH lakes were acclimated to incubation lake conditions by replacing 25% of the holding water each day with that of the incubation lake water. Five individuals were placed into each cage, and transferred into the incubation lakes on May 19–20. The number of eggs laid and adult survival were checked weekly. Eggs were first noted when water temperatures rose above 12–14°C (mid to late May for the study lakes). Adults were brought to the laboratory on June 17 for shell length and sex determination, and were returned to the lakes on June 18. Shell length was determined as the distance from the apex to the lower lip of the aperture and was measured to the nearest 0.1 mm with an ocular grid in a Wild Leitz dissecting microscope. Males were identified by the presence of a copulatory organ (verge) located behind the head region on the dorsal surface. Cages were retrieved on August 19–22, when final egg counts were determined. The number of hatchlings was documented after 53 (SE ± 1.5) and again after 89 (SE ± 1.2) days following initial incubation.

Average fecundities were calculated for each cage by dividing the total number of eggs by the number of adult females present. Percentage survival was determined after 52 and 89 d as the number of newly hatched individuals × 100 divided by the number of egg capsules per cage. An examination of the residuals showed that no transformation was necessary for the fecundity data, and that an arcsin square root transformation normalized the percent survival data. Fecundity and percent survival data were analyzed separately as 3 by 5 factorial Analysis of Variance (ANOVA), the factors being source lake (3) and incubation lake (5). Protected least significant difference (LSD) tests ($p = 0.05$) were employed to determine which treatment means were significantly different. All statistical analyses were performed using SAS (1982) on an IBM PC.

Water samples were collected approximately biweekly throughout the summers of 1985 and 1986 in thrice rinsed 500-ml polyethylene bottles. Sample pH and total inflection point alkalinities were determined by the Ontario Ministry of the Environment at Dorset, Ontario. Twice in 1985 and once in 1986, duplicate water samples were submitted in rinsed, 500-ml, clear polyethylene bottles to the Ministry of the Environment laboratory (Rexdale, Ont.) for major ion and nutrient analyses (OME 1981).

Assessment of Hatching Success

In 1986, snails were incubated in the five lakes chosen for the transplant experiment, and a very acidic lake (Bat Lake, pH 4.62) to further examine the hatching process in *A. limosa*. In 1985, no differences in the percent survival of offspring from females reared in different lakes were found after 89 d (source lake effect). Therefore, all adults for transplant in this experiment were sampled from Green Lake (pH 7.67) where high densities reduced the amount of collection time required.

Snails were collected on May 6, 1986 and brought to the laboratory where one female and one male were randomly selected for transplant into a cage. The cages were lined with glass microscope slides so that eggs could be transferred easily. The number of cages introduced per lake was doubled to 10 to get a more precise estimate of reproductive success. Adults were placed in the six lakes on May 23–24, and cages were examined for the presence of eggs every 3–5 d. As soon as 10 eggs had been laid, the glass slides upon which they were attached were transferred to a second set of cages so that embryo development, hatching success, and juvenile survival could be followed more closely. Several adults were also held in Bat Lake water in the laboratory to examine embryonic development more closely under acidic conditions.

All cages were removed to the laboratory in mid July (17–22) and hatchlings were counted and held for use in a hatchling survival experiment. One hundred egg capsules from the cages in each lake were examined under the microscope for evidence of hatching (except in the case of Bat Lake where few eggs were laid). The presence of a tear in the egg capsule provided evidence of successful hatch as *A. limosa* embryos emerge by chewing their way through the capsule wall with their radula (Davis 1961).

Percentage hatch data were normalized using an arcsine square root transformation, and the number of successfully hatched embryos in each lake was compared using a one-way ANOVA and protected LSD tests.

Hatchling Survival and Growth

Newly hatched snails were retrieved from the cages used to determine hatching success on July 17–22, 1986. Ten juveniles

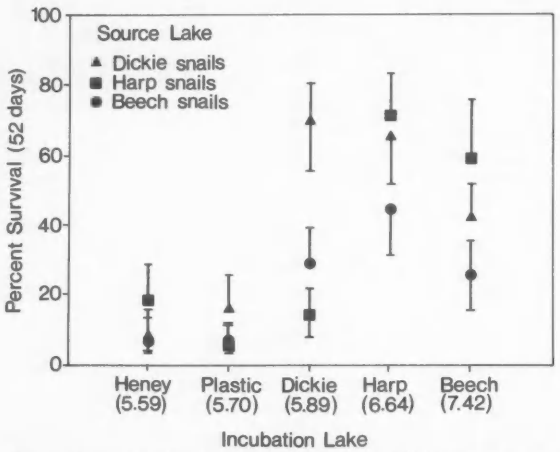

FIG. 2. Percentage survival (No. hatchlings × 100·No. egg capsules per cage^{-1}) of *Amnicola limosa* incubated in lakes for 52 d. Vertical bars represent standard errors of the mean. Values in brackets represent lake pH.

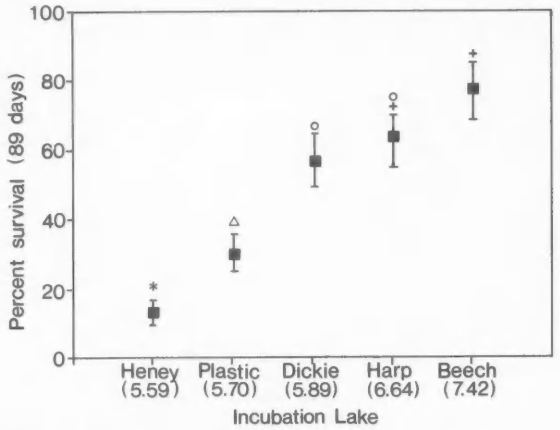

FIG. 3. Percentage survival (No. hatchlings × 100·No. egg capsules per cage^{-1}) of *Amnicola limosa* incubated in lakes for 89 d. Means with the same symbol are not significantly different from each other ($p < 0.05$). Vertical bars represent standard errors of the mean. Values in brackets represent lake pH.

were randomly chosen from the offspring of the 10 females (100 total) from each lake, except in Bat Lake (pH 4.62) where no hatchlings were found, and in Heney Lake (pH 5.59) where only 80 surviving offspring were counted. All hatchling shell lengths were measured to the nearest 0.1 mm before transfer to a set of 100-mL polyethylene containers with mesh sides. Ten juveniles were transplanted into each of 10 cages per lake on July 30 to August 5. Cages were retrieved on September 17 and brought to the laboratory where the number of live hatchlings were recorded, and their shell lengths measured. Shell growth rates were expressed in mm·d^{-1}.

The mean number of surviving offspring from each cage was calculated and the results from each lake were compared using ANOVA and LSD tests, for both the July and September data. Percent survival data were normalized using an arcsine square root transformation. Two, one-way unbalanced ANOVA's followed by LSD tests were employed to analyze the initial and final shell length data for surviving juveniles from each lake. To determine if growth rates differed between lakes, an analysis of covariance was used with the difference between final and initial shell lengths (growth) as the dependent variable, and initial shell length as the covariate. All length and growth data were logged before statistical analysis.

Predicted Recruitment

Data from field observations were combined in an attempt to reconstruct the possible events leading to the reproductive failure of *A. limosa* observed in 1980 in Heney Lake (Rooke 1983). Predicted recruitment was compared for Heney Lake (pH 5.59) and an unaffected circumneutral lake (Harp, pH 6.64).

Measured densities of mature *A. limosa* in the littoral zones of each lake for 1980 were obtained from Rooke (1983). Densities of females were determined from observed ratios of females to males (M.A. Shaw unpubl. data). Using a lake pH–fecundity relationship determined for indigenous populations of this gastropod (Shaw 1987), fecundities were empirically predicted for each lake. The hatching success and juvenile survival data presented in this paper were used to predict the number of offspring·m^{-2} in mid September in Heney and Harp Lakes.

Results

Transfer of Adults Among Lakes

A positive trend between lake pH and fecundity was found for snails in the transfer experiment. There was a highly significant difference in the number of eggs laid per female between the source lakes ($p < 0.001$), but no differences due to an incubation lake effect ($p = 0.766$). Snails collected from the highest pH/alkalinity lake (Beech Lake) had significantly higher fecundities than those from Dickie and Harp Lakes ($p < 0.01$). Average fecundities (No. eggs·female^{-1}·season^{-1}) were 59.16 in Beech Lake (pH 7.42), 41.66 in Harp Lake (pH 6.64), and 41.62 in Dickie Lake (pH 5.89).

There were significant differences in the percent survival among lakes 52 d after incubation (Fig. 2). The incubation lake effect was highly significant ($p < 0.0001$). Differences due to a source lake effect were also significant ($p = 0.0310$) as was the interaction term ($p = 0.0436$). The percentage survival of embryos incubated in Heney and Plastic Lakes was lower than those in the three lakes which supported viable *A. limosa* populations. Of snails incubated in Dickie Lake (pH 5.89), those from Dickie exhibited higher hatchling survival than the snails from the other two source lakes.

After 89 d of incubation those embryos held in the two lowest pH lakes had a significantly lower percent survival ($p < 0.0001$) (Fig. 3). Survival of embryos in Dickie and Harp Lakes was not significantly different, while those incubated in the highest pH lake (Beech Lake) exhibited the highest success. There was no longer an effect due to source lake ($p = 0.882$).

Hatching Success

Females collected from Green Lake exhibited similar fecundities over a pH range of 5.59 to 7.42 (Table 2). However, individuals incubated in Bat Lake (pH 4.62) laid very few eggs, and all embryos failed to hatch in the field and in the laboratory at this pH. Hatching success ranged from 88–97% in the remaining five lakes (Table 2). No significant differences in percent hatch among lakes were found ($p = 0.4210$).

TABLE 2. Average fecundity (No. eggs·female^{-1}·d^{-1}), percentage hatch, percentage hatchling survival, and average juvenile growth rates (mm·d^{-1}) of *A. limosa* collected from Green Lake (pH 7.67) and incubated in the six study lakes. Values underscored by the same line are not significantly different ($p < 0.05$).

	Lake (pH)					
	Bat (4.62)	Heney (5.59)	Plastic (5.70)	Dickie (5.89)	Harp (6.64)	Beech (7.42)
Fecundity	0.13	1.45	1.58	1.83	1.34	1.68
Percent hatch	0.00	90.1	88.0	96.7	92.0	87.8
Percent survival (mid July)	—	22.7	34.3	36.2	56.7	68.7
Percent survival (mid Sept.)	—	25.0	50.0	65.0	68.0	72.0
Growth rate (mm·d^{-1})	—	.0103	.0079	.0074	.0117	.0101

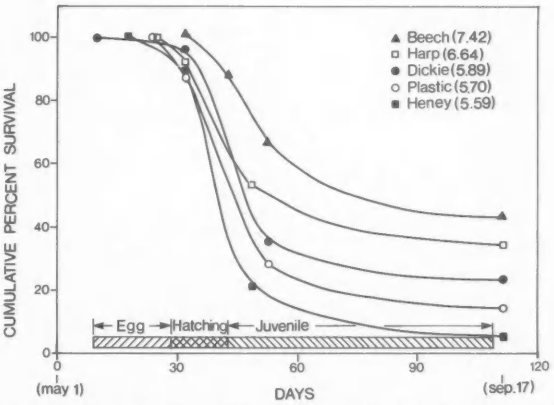

FIG. 4. Cumulative percentage survival of egg and hatchling stages of *Amnicola limosa* incubated in lakes ranging in pH from 5.59 to 7.42, from mid-May to mid-September, 1986. Values in brackets represent lake pH.

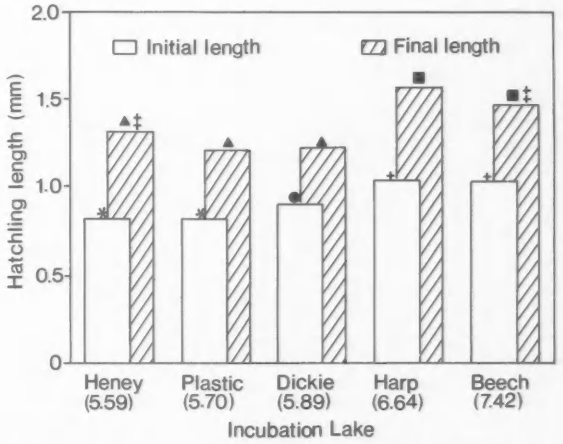

FIG. 5. Initial and final shell lengths (millimetres) of surviving *Amnicola limosa* juveniles incubated for 43 to 49 d in the five study lakes. Bars followed by the same symbol are not significantly different from each other ($p < 0.05$). Values in brackets represent lake pH.

Hatchling Survival and Growth

There was a positive trend between hatchling survival and lake pH. In mid July, differences between lakes were highly significant ($p = 0.0019$) with survival ranging from 22.7% at pH 5.59 to 68.7% at pH 7.42. (Table 2). Similarly, hatchling survival ranged from 25.0 to 72.0% in Heney and Beech Lakes, respectively in mid September, and lake effect differences remained significant ($p = 0.0012$) (Table 2).

The results of the combined data on offspring viability from the egg stage (late May) until mid September are plotted in Fig. 4. On average, 5.1% of the embryos survived in Heney Lake (pH 5.59), compared with a survival rate of 44% in Beech Lake (pH 7.42). The greatest period of mortality occurred within 20 d posthatch.

There were also significant differences in the size of hatchlings in the five lakes, immediately following hatch ($p < 0.0001$) and in mid September ($p < 0.0001$). The initial shell lengths of individuals from Heney and Plastic Lakes were on average 0.20 mm (20%) smaller than those from Harp and Beech Lakes (Fig. 5). At the completion of the growth experiment, juveniles from Plastic, Dickie, and Heney Lakes averaged 0.25 mm smaller than those in the circumneutral lakes,

TABLE 3. Predicted recruitment of *Amnicola limosa* in Heney (pH 5.59) and Harp (pH 6.62) Lakes.

	Lake	
	Heney	Harp
Density of adults (No.·m^{-2}) (Rooke 1983)	2.2	6.0
Density of females (F:M = 1.4:1) (Shaw 1987)	1.28	3.49
Predicted fecundity (No. eggs·female^{-1}) (Shaw 1987)	22	42
Eggs·m^2·season^{-1}	28.2	146.6
Percent survival to mid Sept.	5.1	35.5
Density of surviving offspring in Sept. (No.·m^2)	1.4	52.0

although differences were not as highly significant as at the start of the experiment (Fig. 5). Growth rates were not significantly different between lakes ($p = 0.0699$) (Table 2).

Predicted Recruitment

The predicted recruitment of *A. limosa* in Heney and Harp Lakes are compared in Table 3. The abundance of juveniles surviving in mid September is approximately 35 times greater in the circumneutral lake (Harp) than in the low alkalinity lake (Heney). Even assuming 100% survival of juveniles to sexual maturity (approximately 20 mo based on Rooke's (1983) findings), and no losses due to predation, *Amnicola* populations would decline to undetectable levels ($<1 \cdot m^{-2}$) in Heney Lake within 3 yr. Surveys in 1982 and 1983 (M. Stephenson, AECL, Pinawa, Manitoba R0E 1L0, unpubl. data) show that in fact the Heney Lake *A. limosa* population has declined. An examination of 30 Ekman grab and 40 sweep samples from littoral areas previously known to harbour *A. limosa* yielded one adult specimen in 1985 (M. A. Shaw unpubl. data). Extensive sampling in 1980 (Rooke 1983) showed that *A. limosa* was also very rare in Plastic Lake (pH 5.70). No specimens were found in subsequent analysis of 30 Ekman grab samples from Plastic Lake in 1985 (M. A. Shaw unpubl. data).

Discussion

There was no evidence to suggest that the failure of females to oviposit contributes to decreased recruitment in lakes currently experiencing reproductive failure of *A. limosa*. Only when snails were held at pH 4.62 were drastic reductions in fecundity apparent. However, the transfer experiment showed that adults from higher pH/alkalinity environments laid significantly more eggs than those from lower pH lakes. Recruitment of transplanted individuals in the two low-pH lakes from which *A. limosa* had recently disappeared or was rare was shown to be significantly lower than in three lakes supporting viable populations. There was no indication that the offspring of adults reared at pH 5.90 (Dickie Lake) differed in their response to acclimation at low pH (5.59–5.70) than Beech Lake (pH 7.42) or Harp Lake (pH 6.42) offspring. The substantial increase in recruitment of Beech and Harp Lake offspring reared in Dickie Lake water between 52 and 89 d may have been due to delayed hatch. Both Servos et al. (1985) and Shaw (1987) have documented delayed hatch of *A. limosa* embryos held in the laboratory at pH 5.5.

Evidently, the poor recruitment of *A. limosa* in Heney and Plastic Lakes was not due to a failure of eggs to hatch, as hatching success was found to be relatively constant (88–97%) in lakes ranging in pH from 5.59–7.42. Servos (1983) documented comparable hatching rates for this species in a laboratory study at pH 5.5 and 6.5, while eggs held at or below pH 5.0 failed to hatch. Similarly, embryos held at Bat Lake water (pH 4.62) in this study suffered complete mortality prior to hatch.

The most critical stage in the life cycle of *A. limosa* appears to be the newly hatched stage with the greatest period of mortality occurring within 20 d posthatch. Survival rates for *A. limosa* ranged from 23% at pH 5.59 to 69% at pH 7.42 during this period. By 1 mo posthatch, mortality rates appeared to stabilize. Servos and Mackie (1986) reported that mortality of 1- and 2-yr old snails was very low, even during rapid pH depressions associated with spring snowmelt. Size-selective mortality at low pH has been found for other gastropods as well. Juveniles of the snail *Physella heterostropha* have been shown to experience complete mortality after 14 d at pH 4.0, while mature individuals appeared to be unaffected (Allan and Burton 1986).

Under natural conditions, most gastropod survivorship curves are characterized by high mortality during embryonic and/or juvenile stages (Hunter 1961). Dewitt (1954a,b) reported 70% mortality during the egg stage of the pond snail *Physa gyrina*. Documented mortality rates for hatchlings averaged between 52 and 53% for the land snail *Cepaea nemoralis* (Wolda and Kreulen 1973) and *Viviparus georgianus* (Browne 1978) to 90% for young *Physa fontinalis* (Dewitt 1955). The pond snail *Lymnaea elodes* has been found to experience a combined mortality of 97.8% during the egg and juvenile stages (Eisenberg 1966). In this study, the combined mortality of juvenile *A. limosa* in two circumneutral lakes ranged from 56 to 64%. However, there was an order of magnitude difference between the seasonal (mid-May to mid-September) recruitment in the most acidic lake (5.1% at pH 5.59) and the highest pH lake (44% at pH 7.42).

In addition to the high hatchling mortality in *A. limosa*, hatchling shell lengths were also found to be significantly smaller at low pH. Hatchlings reared in Heney and Plastic Lakes were on average 20% smaller in shell length than those in circumneutral Harp and Beech Lakes. However, the final shell lengths of juveniles incubated in the two lowest pH lakes were probably overestimated, as average values were based on the 25 and 50% of individuals which survived until mid September in Heney and Plastic Lakes, respectively. Given the apparent size-selective mortality in this species, average growth rates for these two lakes are probably biased upwards. Rooke (1983) and Servos et al. (1985) showed that growth of first and second year *A. limosa* was significantly reduced in low alkalinity waters. Differences in growth rates may be due to a number of factors. Several authors have suggested that the energy required to maintain blood ionic composition in fish is greater at low pH than at circumneutral pH (Eddy 1975; Havas 1981; Muniz and Leivestad 1980). Since low-pH lakes typically have low calcium concentrations, the energy involved in the maintenance and growth of mollusc shells may also be greater. It is possible that changes in diatom species and abundance in acidifying lakes could contribute to a lower quality and/or quantity of suitable food for *A. limosa*. Any combination of these stresses would result in less energy available for growth at low pH.

The implications of reduced survival and size of juveniles in low pH lakes are two-fold. Firstly, fewer numbers of offspring would survive to sexual maturity below pH 5.70. In addition, the smaller size of juveniles indicates that a longer time would be required for these individuals to grow to reproductive size. These two factors would be responsible for reductions in the recruitment of future generations.

A comparison between predicted recruitment and measured densities in Heney Lake indicates that the observed recruitment failure in 1980 has resulted in a depauperate population and the possible elimination of *A. limosa*. Evidence presented here suggests that recruitment failure due to reductions in fecundity and hatchling survival are responsible for the disappearance of this species from Heney Lake, and possibly from other low pH lakes as well.

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Mitochondrial DNA Sequence Similarity of Atlantic and Pacific Albacore Tuna (*Thunnus alalunga*)

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Restriction endonuclease analysis of mitochondrial DNA purified from 11 south Atlantic (Capetown, South Africa) and 12 north Pacific (San Diego, USA) albacore tuna (*Thunnus alalunga*) revealed no restriction sites which could distinguish an Atlantic from a Pacific albacore. Although restriction site variation was found within the pooled sample, variants were found only in single fish. These results suggest either recent isolation of Atlantic and Pacific albacore or, more likely, at least a small amount of migration between the two ocean basins.

Une analyse par endonucléase de restriction de l'ADN mitochondrial purifié à partir de 11 thons (*Thunnus alalunga*) de l'Atlantique sud (Capetown, Afrique du Sud) et de 12 thons du Pacifique nord (San Diego, É.-U.) n'a révélé aucun site de restriction permettant de distinguer un thon de l'Atlantique d'un thon du Pacifique. Bien qu'on ait trouvé des variations dans les sites de restriction dans l'échantillon réuni, les variants ne se retrouvaient que chez des poissons isolés. Ces résultats indiquent soit un isolement récent des thons de l'Atlantique et du Pacifique ou, plus probablement, au moins une certaine migration entre les deux bassins océaniques.

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Fishery stocks, although not necessarily defined with genetic criteria, are usually assumed to have an underlying genetic basis (Gulland 1971). A stock boundary is indicated by significant differentiation of morphological, physiological, or biochemical characters between fish from different sampling sites and these characters are assumed to be under direct genetic control. Similarly, a marked change between geographic areas in catch per unit effort, mark and recapture returns, or other fishery statistics can also be used to define a stock boundary. A problem in fishery management arises, however, when fish from different putative stocks, defined on the basis of fishery statistic criteria, or fish from geographically distant areas cannot be distinguished with an analysis of genetic characters. The albacore (*Thunnus alalunga*) in the north Pacific Ocean presents such a problem.

Considerable effort has been expended on mark and recapture studies of albacore in the north Pacific Ocean to elucidate movement patterns. Basically, there appear to be two distinct groups of albacore which migrate to the western coast of North America. These groups differ in modal sizes of year classes, growth rates, movements, and areas of occurrence (Laurs and Lynn 1977; Laurs and Nishimoto 1979; Laurs and Wetherall 1981). Those fish which arrive at the California coast south of 40°N are slightly larger and have a faster growth rate than those which arrive at the coast north of 40°N (Laurs and Wetherall 1981). Furthermore, the northern group appears to migrate to the western north Pacific where it is vulnerable to the Japanese surface and subsurface fisheries, whereas the southern group tends to be recaptured in the central north Pacific. Although there is a slight interannual leakage between northern and southern groups (Laurs and Nishimoto 1979) the vast majority of recaptures of tagged fish has been from the area of marking. It is not known when fish leave the north Pacific surface fishery, but few mature adults are found in the temperate eastern Pacific, and spawning, as evidenced by ripe females and young larvae, seems mostly confined to the tropical central Pacific (Sund et al. 1981).

On the basis of mark and recapture data, modal sizes of year classes and growth rates of tagged fish, Brock (1943); Laurs and Lynn (1977); and Laurs and Wetherall (1981) have proposed that the two groups of albacore in the north Pacific represent distinct subpopulations. It is not known if fish from the putative northern and southern north Pacific albacore subpopulations remain reproductively isolated in the common spawning area or comprise genetically distinct stocks. To elucidate the genetic basis of population structure of the north Pacific albacore, an extensive genetic survey with considerable effort expended on sampling albacore on a large spatial and temporal scale will most likely be necessary. Before committing resources to such a task, we felt it would be beneficial to first determine the magnitude of genetic differentiation between albacore of different ocean basins. An estimate could then be made of the sampling effort required to detect genetic differentiation between the closely related putative subpopulations within the north Pacific.

In this paper we report that a genetic analysis of a small sample of albacore from Capetown, South Africa and San Diego, California employing restriction endonuclease analysis of mitochondrial DNA (mtDNA) revealed no significant genetic differentiation between albacore from the different ocean basins. This result is compared with other mtDNA studies and the

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TABLE 1. Fragment sizes produced by restriction endonuclease digestion of mtDNA purified from albacore tuna from Capetown, South Africa and San Diego, United States. Not all of the smaller fragments were scored with the *Hinf* I and *Msp* I digestions.

Restriction endonuclease	Pattern	Fragment sizes	Sample pattern San Diego	Size and distribution Capetown
Ava I	A	7.6, 4.7, 4.4	10	6
Bam HI	A	14.0, 2.8	8	7
	B	7.0, 7.0, 2.8	—	1
Bst EII	A	12.4, 4.4	4	4
Eco RI	A	8.8, 8.0	8	9
Hinc II	A	3.5, 3.1, 2.9, 2.7, 1.8, 1.6, 1.2	10	9
Hind III	A	4.9, 3.8, 3.0, 1.6, 1.3, 1.2, 0.9	8	9
	B	8.7, 3.0, 1.6, 1.3, 1.2, 0.9	1	—
	C	4.4, 3.8, 3.0, 1.6, 1.3, 1.2, 0.9, 0.5	1	—
Hinf I	A	4.8, 1.2, 1.1, 0.83, 0.71, 0.64, 0.60, 0.51, 0.48, 0.42	3	3
Msp I	A	3.5, 1.4, 1.3, 1.2, 1.1, 0.95, 0.72, 0.56, 0.40	3	3
Pst I	A	10.4, 3.7, 2.7	10	8
	B	14.1, 2.7	1	—
Pyu II	A	8.4, 4.0, 2.7, 1.7	8	6
Sin I	A	8.0, 4.8, 1.3, 1.1, 0.8, 0.7	8	8
	B	7.0, 4.8, 1.3, 1.1, 1.0, 0.8, 0.7	1	—
Xba I	A	9.2, 4.6, 3.0	6	6
Xho I	A	12.0, 4.8	6	6

implications of this investigation are discussed in reference to management of the albacore fishery.

Materials and Methods

Albacore were collected by hook and line (both by trolling artificial lures and live bait fishing) off San Diego, California in July and August 1984 ($n = 11$) and off Capetown, South Africa, in January 1983 ($n = 6$) and February 1985 ($n = 6$). Shortly after capture, liver and gonads were removed from the fish, rinsed in cold buffer (10 mM TRIS pH 7.5, 50 mM EDTA, 250 mM KCl) and quickly frozen on dry ice or in liquid nitrogen. Tissue samples were shipped to the laboratory in liquid nitrogen or on dry ice. Specimens were stored at −75°C until processing.

Preliminary mtDNA analyses were carried out on another scombrid, the chub mackerel, *Scomber japonicus*, to determine optimal tissues for preparing mtDNA as well as to optimize procedures for sample rinsing, freezing, and storage. Highest mtDNA yields in *S. japonicus* were obtained from fresh mature ovaries, although substantial yields were also obtained from fresh liver tissue. Yields of mtDNA decreased with tissue freezing, but were still adequate from liver and ovarian tissues immediately frozen in liquid nitrogen or on dry ice. Rinsing tissues in the cold buffer described above increased yields of closed-circular mtDNA.

We purified mtDNA using CsCl density gradient centrifugation following the protocols presented in Lansman et al. (1981). Restriction endonuclease digestion of purified albacore mtDNA was performed with the following enzymes: *Ava* I, *Bam* HI, *Bst* EII, *Eco* RI, *Hinc* II, *Hind* III, *Hinf* I, *Kpn* I, *Msp* I, *Pst* I, *Pvu* II, *Sin* I, *Xba* I, and *Xho* I. All restriction enzymes were purchased from Bethesda Research Laboratories (BRL), except *Sin* I which was purchased from Sigma Chemical Company, and were used according to the manufacturer's directions. Because of small mtDNA yields from some samples it was not possible to survey each sample with every restriction endonuclease. Sample sizes for each enzyme are presented in Table 1.

Endlabelling of the restriction fragments with radioactive nucleotide triphosphates followed the protocols of Brown (1980) with the exception that we did not find it necessary to ethanol precipitate endlabelled mtDNA fragments resulting from digestion with restriction endonucleases that recognize six nucleotide base pairs. Restriction fragments were separated by size on 1.0% agarose horizontal gels and 3.5–5.0% polyacrylamide vertical gels run at 3 $V \cdot cm^{-1}$ overnight. Gels were dried after electrophoresis, covered with plastic wrap and autoradiographed for 2–24 h without screens at room temperature. Restriction fragment sizes were determined by comparison with commercial size standards (BRL 1 Kbp and 123 bp ladders) run in duplicate or triplicate on each gel.

Results

Results of the restriction endonuclease analysis of albacore mtDNA are summarized in Table 1. Of the 13 restriction endonucleases used in this study, 12 were informative in the sense that they cleaved the circular mtDNA molecule in more than a single site, producing at least two fragments. Restriction fragment length polymorphisms were detected with digestions of *Bam* HI, *Hind* III (2 variants), *Pst* I, and *Sin* I. In all cases each variant was found in a single individual and represented the gain or loss of a single cleavage site from the common pattern. No restriction fragment length polymorphisms were found within a pooled sample of six albacore using *Hinf* I or *Msp* I, restriction enzymes which recognize four nucleotide base pairs. The mtDNA from only three individuals from each ocean was suitable for analysis with these enzymes, which produced several small fragments, because high background counts obscured the smaller fragments in the other individuals.

The size of the albacore mitochondrial genome was estimated by summing the fragment lengths produced by those restriction enzymes that resulted in DNA fragments in the linear (sensitive) region of the size standard. Analysis of fragment sizes resulting from digestions with *Ava* I, *Eco* RI, *Hinc* II, and *Hind* III produced a mean genome size of $16\,750 \pm 200$ nucleotide base pairs for the albacore mitochondrial genome (Table 1). This value lies within the 16 300 to 19 800 base pair range reported for other fish mtDNAs (Avise et al. 1984; Berg and Ferris 1984; Graves et al. 1984; Beckwitt and Petruska 1985; Bentzen et al. 1988).

Discussion

No significant mtDNA sequence differentiation was demonstrated between albacore caught off San Diego, California

and those caught off Capetown, South Africa. There were no restriction fragments which could be used to distinguish north Pacific from south Atlantic albacore. Six restriction fragment length polymorphisms were detected within the pooled sample of 23 individuals. Each of these variants was present in only one individual, and no individual from either ocean was variant for more than a single site.

On the basis of the results obtained in this study, it is not possible to disprove the null hypothesis that albacore from the north Pacific and south Atlantic share a common gene pool. This statement does not preclude the possibility that some genetic differentiation exists between fish from the two ocean basins — a larger investigation, surveying more individuals or enzymes per individual, might demonstrate some mtDNA differentiation. However, with the sample sizes used in this study, both the number of individuals and restriction fragments surveyed, no interocean mtDNA sequence differentiation was detected.

To obtain a relative estimate of the degree of intraspecific differentiation within the albacore population, the results of this study can be compared with the results from other investigations of mtDNA differentiation within vertebrates. At a level of analysis comparable with the present study, both in numbers of individuals and restriction fragments surveyed, significant intraspecific differentiation has been demonstrated in pocket gophers of different counties (Avise et al. 1979), deer mice of different counties (Lansman et al. 1983), and different coastal islands (Ashley and Wills 1987), cotton rats of the same field (Kessler and Avise 1985), bluegill within the same drainage system (Avise and Saunders 1984; Avise et al. 1984), cutthroat trout from different drainage systems (Gyllensten et al. 1985), horseshoe crabs of the Atlantic and Gulf coasts of Florida (Saunders et al. 1986), and toadfishes of the Atlantic coast of the United States (Avise et al. 1987). No such differentiation was found between albacore of the north Pacific and south Atlantic.

The lack of significant mtDNA sequence differentiation between north Pacific and south Atlantic albacore is similar to results reported for the American eel (*Anguilla rostrata*) along the Atlantic coast of North America (Avise et al. 1986) and for skipjack tuna (*Katsuwonus pelamis*) sampled in the Pacific and Atlantic Oceans (Graves et al. 1984). In the case of the American eel, the lack of differentiation probably results from the unusual spawning migration of the fish which may form a single panmictic population (Avise et al. 1986), while the skipjack tuna mtDNA similarity may result from migration between ocean basins (Graves et al. 1984).

While only a few studies have investigated intraspecific mtDNA sequence variation within marine fishes, low levels of intraspecific genetic differentiation of nuclear gene products have been demonstrated for several marine species. In a protein electrophoretic investigation of the milkfish (*Chanos chanos*) Winans (1980) found no significant genetic differentiation between fish sampled over a range of 10 000 km. Shaklee (1984) reports low levels of protein variation within the damselfish (*Stegastes fasciolatus*) sampled throughout the Hawaiian Archipelago, a distance of about 2500 km. Rosenblatt and Waples (1986) found little genetic differentiation between dolphin fish (*Coryphaena hippurus*) of the Pacific and Atlantic or within several species of reef fishes with distributions across the tropical Pacific.

The low level of intraspecific nuclear and mtDNA genetic differentiation observed in these marine fishes may be the result of several factors, but high dispersal ability and a lack of geographic isolating mechanisms in the pelagic environment are probably the most important. Many marine fishes have long-lived pelagic eggs and larvae which are capable of long-range dispersal, and for several of the strong swimming pelagic fishes, such as the tunas and dolphin fish, the ability for long-range dispersal continues throughout the adult life. The great dispersal abilities of these fishes in the pelagic environment, which is essentially free of geographic isolating mechanisms, would tend to result in an increase in intraspecific genetic homogeneity.

The lack of significant intraspecific mtDNA sequence differentiation between north Pacific and south Atlantic albacore encountered in the present study indicates that the two groups have either been separated for a very short time or maintain some form of genetic contact. If gene flow is occurring between albacore of the different ocean basins, then a suitable habitat and mechanism for exchange must exist. Although juveniles of northern and southern oceans are found in northern and southern temperate feeding grounds respectively, adults move toward the tropics to spawn. Tropical spawning seasons are temporally displaced in the northern and southern hemispheres (Sund et al. 1981) and it is not known if there is leakage of adults between spawning areas. Catch rates of albacore are significantly depressed near the equator; however, positive catches during different seasons across the equator in the western Pacific indicate that the distribution of albacore may at times be continuous (Foreman 1980). In the southern oceans albacore are taken as far south as 45°S in waters above the west wind drift. As albacore from all three southern oceans may be feeding in these waters, there is ample opportunity for exchange between southern ocean basins via the Indian Ocean.

The number of albacore needed to migrate between ocean basins to prevent genetic differentiation from accumulating is very small. Theoretical models of nuclear gene product differentiation (Allendorf and Phelps 1981) or mtDNA differentiation (Takahata and Palumbi 1985) indicate that migration on the order of individuals per generation is sufficient to prevent genetic differentiation. This gene flow does not have to be constant and does not have to represent the long migration of any individual fish; rather, it can be periodic and occur as several short exchanges. Inasmuch as albacore in all oceans move to the tropics to spawn, the possibility of such exchanges in matings between fish from different areas seems likely.

This study was undertaken to determine the magnitude of mtDNA sequence differentiation between north Pacific and south Atlantic albacore so that we could estimate the sampling effort required to separate possible stocks within the north Pacific. If the variant mtDNA restriction patterns found in single albacore of one ocean in this study represent real differences in the presence and absence of mtDNA clones between albacore of the north Pacific and south Atlantic (and are not artifacts of sampling error), a considerably larger sample size from each ocean would be required to statistically distinguish the populations. Such an investigation is certainly feasible; however, assuming that intraocean genetic differentiation is considerably less than interocean differentiation, a sampling effort of tremendous magnitude would be required to determine if genetic differentiation exists between putative albacore stocks within the north Pacific. Rather than commit resources to such a study at this time, we believe that a reevaluation of the problem is warranted.

The results of this analysis indicate that there is a high degree of mtDNA sequence similarity between albacore of the north Pacific and south Atlantic. Although albacore of the north Pacific and south Atlantic may represent a single, homogeneous stock to the population biologist, they do not represent a single management unit to the fishery biologist. While the level of gene flow between ocean basins may be sufficient to prevent significant genetic differentiation from accumulating, it is doubtful if the gene flow represents even a minor fraction of the total population. On a smaller scale, the two putative populations of albacore which reach the west coast of North America may have as much as 4% interannual leakage (Laurs and Nishimoto 1979). While 4% interannual exchange between fish returning north or south of 40°N represents a significant gene flow on an evolutionary time scale to the population biologist, it also represents a significant stock boundary to the fishery biologist. The problem may be semantic, but it is indicative of a current misunderstanding of the role of genetic analyses in fishery management. If genetic differentiation can be demonstrated between two fishery units separated on the basis of fishery statistics or geographic location, they are distinct stocks. However, if no genetic differentiation can be demonstrated between these units, they may still be managed as putative stocks, even though they are genetically homogeneous.

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Gear Bias in Field Estimation of the Amount of Food Consumed by Fish

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We made concurrent collections of small (85–100 mm total length) yellow perch (*Perca flavescens*) at the bottom of Lake Erie with an active gear (otter trawl) and a passive gear (gillnet) within a 24-h sampling period. During daylight periods when yellow perch feeding activity was most prominent, gillnetted fish possessed significantly higher median food amounts in stomachs than did trawled fish. Estimated daily food consumption for small yellow perch was 5.86% of body weight by gillnet sampling and 3.98% by trawl sampling. Passive gears tend to sample the most active fish (more likely to be feeding) and may, therefore, yield upwardly biased estimates of food consumption for individuals within a population. Active gears are considered to give more accurate estimates because quiescent and low activity, as well as the more active members of a population, are sampled.

Nous avons capturé concurremment des petites perchaudes (*Perca flavescens*) (85–100 mm de longueur totale) au fond du lac Érié au moyen d'un engin de pêche actif (chalut à panneaux) et d'un engin de pêche passif (filet maillant) au cours d'une période de 24 h. Le jour, lorsque les perchaudes s'alimentent le plus activement, les poisson capturés au filet maillant avaient une quantité d'aliments significativement plus élevée (médiane) dans leur estomac que les poissons capturés au chalut. On estime que les petites perchaudes capturées au filet maillant consomment quotidiennement l'équivalent de 5,86% de leur poids corporel alors que celles capturées au chalut consomment 3,98% de leur poids corporel. Les engins passifs ont tendance à capturer les poissons les plus actifs (probablement en train de chercher de la nourriture) et peuvent donc fausser à la hausse le calcul de la consommation de nourriture des individus dans une population. On considère que les engins actifs permettent d'obtenir une estimation plus précise car ils capturent autant les poissons au repos et présentant une faible activité que les poissons plus actifs au sein d'une population.

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A variety of sampling gears have been used in field estimates of food consumption for fishes. We hypothesized that gillnet sampling (a passive gear tending to collect the most active, more likely feeding, fish) would yield higher point estimates of food amounts in stomachs of a local population of yellow perch (*Perca flavescens*), than would trawl sampling (an active gear presumed to collect active as well as low activity and quiescent, nonfeeding, fish). Our findings suggest that the potential for this kind of gear-related bias should be considered when food consumption studies of fish populations are designed.

Methods and Materials

Yellow perch were collected by bottom trawling for 10 min, every 3 h over a 24-h sampling period at an offshore site in the central basin of Lake Erie in June 1983, prior to thermocline development. The trawl (10.3 m headrope × 10.7 m long, otter trawl) has a mouth width of approximately 5 m when towed at an average speed of 0.75 $m \cdot s^{-1}$, and fishes approximately the bottom 2 m of water. A gillnet strap (91.4 m × 1.8 m) with variable mesh sizes (3.8–7.6 cm, stretch measurement) was fished on bottom within 100 m of the trawling lane during three, 2.5-h periods that temporally bracketed trawl collections made at 1100, 1400, and 2300 h. For example, a gillnet was set at 0945 h and retrieved at 1215 h to bracket the trawl collection that began at 1055 h and ended at 1105 h. Immediately after a trawl or gillnet was retrieved, yellow perch were placed on ice, sorted into bags, and quick-frozen on dry ice. In the laboratory, yellow perch stomach contents were removed, dried (24 h at 80°C), and weighed to the nearest milligram. Dry weights of yellow perch were also determined (72 h at 80°C) so that food amounts in each fish could be expressed as a proportion of dry body weight (weight-specific food amounts, hereafter, termed simply "food amounts").

Food is lost to digestion after capture: the food remaining was assumed to obey the formula $N(t) = N_0 e^{-Rt}$ where t is the time since capture and $R = 0.106$ for the ambient water temperature of 12.6°C (Eggers 1977; Persson 1979). For trawl-caught fish digestive food loss was considered negligible; for gillnet-caught fish we assumed an average $t = 1.25$ h, whence

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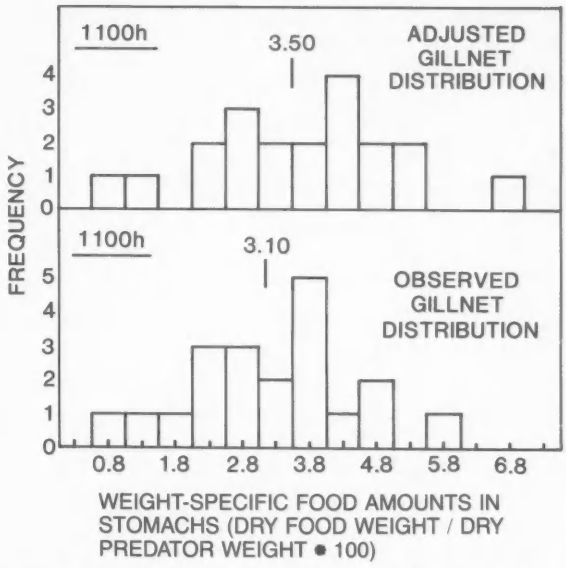

FIG. 1. Comparison of observed distribution (and median) of food amounts in stomachs of yellow perch collected by gillnet (fished from 0945–1105 h) with that resulting after food amounts in each stomach were increased to account for slight digestive losses while fish were in the net. Food amounts were considered to have decreased exponentially over one half the period that gillnets were fished (1.25 h), at the temperature-dependent rate according to Persson (1979).

TABLE 1. Numbers of small yellow perch (85–130 mm total length) collected concurrently by gillnet and trawl from the bottom of Lake Erie during three sampling periods within 24 h, used to compare estimates of food weights in stomach between gear types.

Gear	Midpoint of sampling period		
	2300 h	1100 h	1400 h
Gillnet	11	20	13
Trawl	13	21	15

$N \sim 0.88N_0$. We therefore added 13.6% to each gillnet observations (Fig. 1).

We statistically tested the hypothesis that median food amounts estimated by gillnet collections exceeded medians estimated by corresponding trawl collections, using the nonparametric Fligner–Policello procedure (Fligner and Policello 1981). This test was used because of its relaxed assumptions concerning the relative shapes of any two distributions whose medians are being compared. Finally, we evaluated gear effects on estimates of 24-h food consumption for the local population of small yellow perch. For this evaluation, medians from the sampling distributions of the two gears were entered into a validated correlation model which estimates daily food consumption for yellow perch from only one (or more) point estimate of food amounts in stomachs within a 24-h period (Hayward and Margraf 1987, 1988).

Results

Trawling readily collected yellow perch from 85–200 mm total length (TL); however, gillnet sampling over the relatively short periods collected adequate numbers of fish only in the 85–130 mm TL range for comparisons between the two gears (Table 1). Trawling data at 3-h intervals throughout 24 h showed that feeding activity for these smaller fish was highest at 1100 h, slightly reduced at 1400h, and low (or stopped) by 2300 h (Hayward and Margraf 1987).

Distributions of food amounts in fish collected by the gillnet appeared symmetrical for all three collection periods. In contrast, distributions from trawled fish were positively skewed for the two periods of high feeding activity, but symmetrical for the collection at 2300 h (Fig. 2). Median food amounts among gillnetted fish were significantly greater than for corresponding trawled fish during the two high feeding activity periods ($\underline{\alpha}$ = 0.0008 for 1100 h and 0.0188 for 1400 h) but not so when feeding activity was low ($\underline{\alpha}$ = 0.4681). Estimated 24-h food consumption for the local population of small yellow perch was 5.86% of body weight from gillnet sampling and 3.98% from trawl sampling. We note that even without correcting for digestion, distributions for gillnets showed median food amounts that exceeded trawl-determined medians at marginally significant levels.

Discussion

Our results demonstrate that field estimates of daily food consumption for some fish populations can differ substantially depending on the sampling gear used. Differences in daily food consumption of greater than 1% of body weight are substantial and would be important for most study objectives.

Food amounts in stomachs of yellow perch collected by gillnets were significantly greater than amounts in fish collected by trawling, during periods of higher feeding activity (Fig. 2). This suggests that a group of inactive or less active yellow perch existed, with less food in their stomachs, which were sampled well by the trawl but were less likely to encounter the gillnets. The magnitude of difference in food amounts possessed by distinct activity-level groups at any instant (and, in fact, the existence of distinct groups) may be governed not only by the diurnal feeding stage, but also by food availability, temperature (as it influences gut clearance rates), and feeding mode of the consumers (e.g. continuous versus sporadic). For example, distinct activity-level groups may not be present when food availabilty is low and all individuals must actively seek food. When food availability is quite high, as during our study, however, many individuals may reach satiation and become inactive (or less active) until stomach fullness is substantially reduced. Moreover, at lower temperatures, periods of feeding inactivity may be longer because of slower gut clearance rates and longer times before reinitiation of the urge to feed.

Distributions of food amounts among gillnetted yellow perch were symmetrical (Fig. 2). Skewed distributions of food amounts from trawling reflected some composite of distributions for active (gillnets) as well as for less active individuals which possessed predominantly lower food amounts. Because of this broader coverage, we believe that trawling provided the more accurate estimates of true distributions of food amounts for the local population. The symmetrical distribution of food amounts observed among trawl-collected fish at 2300 h, is expected for low feeding periods when food evacuation exceeds intake rates; greater food quantities in stomachs are reduced most rapidly (exponential decline), resulting in the loss of the distribution's upper tail.

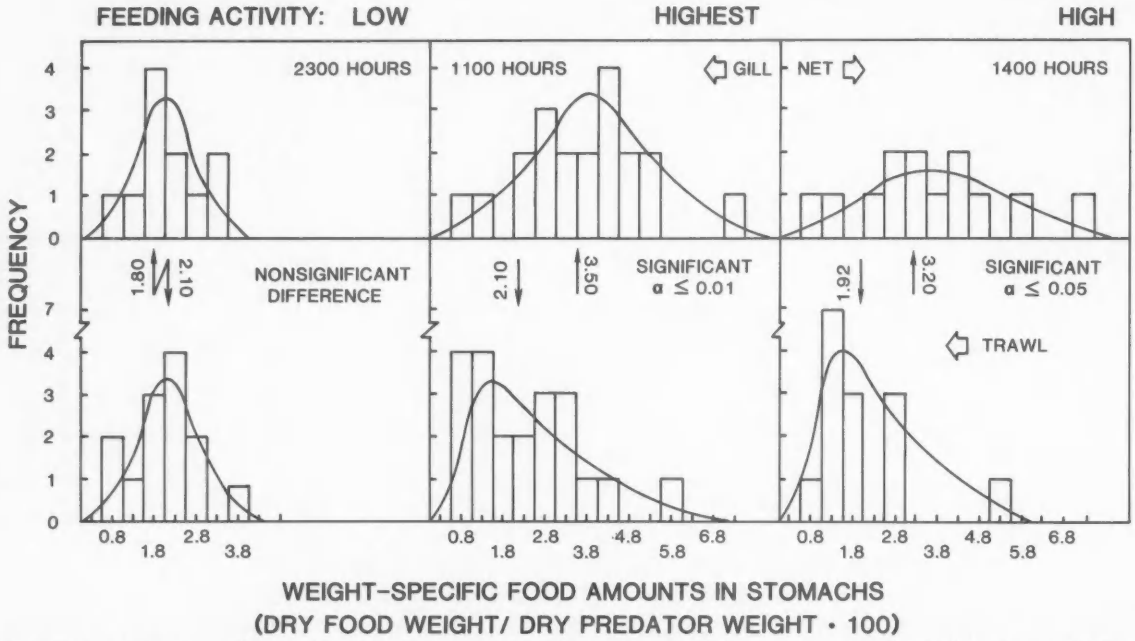

FIG. 2. Comparisons of sampling distributions of food amounts in yellow perch stomachs from concurrent trawl and gillnet bottom collections within a single day in Lake Erie. Vertical arrows and associated numbers indicate median values for each sampling distribution. Probability levels for significant differences between medians from temporally corresponding distributions (trawl versus gillnet) are also given. Curves were fitted by inspection.

An active gear which collects predominantly quiescent or low-activity individuals due to fish avoidance behavior, may yield downwardly biased estimates of median food amounts for the local population. We note that the highest observations of food in stomachs were all in gillnet samples, although the numbers are too small to give more than a tentative hint, and the unbiased medians were unknown. Pragmatism in choice of sampling gears must prevail in field studies of food consumption, because often only one gear type will yield adequate numbers of a targeted fish species or size-group. Nonetheless, our study demonstrates that gear-related bias in estimates of food consumption for fishes can be as important as other sources of error that have received attention. Consideration of this effect is therefore warranted in future field studies. Active sampling gears should be used when practicable, and the possibility of correcting estimates to account for particular gear biases should be explored.

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Characterization of *Aeromonas salmonicida* Strains using DNA Probe Technology

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Epizootiological studies on *Aeromonas salmonicida* are important in view of its role as the causative agent of furunculosis. The use of DNA probes to detect restriction fragment length variations promised to provide a new way to distinguish between different strains of the organism. We used four different DNA probes in combination with seven restriction enzymes to compare seven strains of *A. salmonicida*. Despite the diversity of the geographical origins of the organisms no differences in the patterns of the hybridizing bands were found. This suggests that the DNA sequences of *A. salmonicida* are very strongly conserved and that the potential for DNA probes to identify different strains may be limited.

Les études épizootiques sur *Aeromonas salmonicida* sont importantes dans la mesure où cet organisme est responsable de la furonculose. L'utilisation de sondes d'ADN pour déceler les variations dans la longueur des fragments de restriction semblait une méthode prometteuse pour distinguer les différentes souches de l'organisme. Nous avons utilisé quatre sondes d'ADN différentes et sept enzymes de restriction pour comparer sept souches de *A. salmonicida*. En dépit de la diversité de l'origine géographique de l'organisme, nous n'avons observé aucune différence dans le profil des bandes d'hybridation. Ces résultats donnent à penser que les séquences de l'ADN de *A. salmonicida* sont protégées de façon très efficace et que l'utilisation des sondes d'ADN pour identifier différentes souches risque d'être limitée.

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Aeromonas salmonicida is the causative agent of furunculosis, a disease which affects many species of fish and is of major importance in salmonid farming. The absence of an efficient selective medium and its poor plating efficiency in mixed cultures (McCarthy 1977), has hampered studies on the ecology of this bacterium. It is known, however, that this organism primarily resides in freshwater, probably in asymptomatically infected fish, but the possibility of persistence in river sediments has also been considered (McCarthy and Roberts 1980). The organism is thought to enter into hatcheries via the intake water. The remarkable homogeneity of the organism with respect to biotype (Smith 1963; Schubert 1967), plasmid profile (Toranzo et al. 1983), and serotype (Paterson et al. 1980) has inhibited subspecies strain identification and, therefore, detailed epizootiological studies.

Because the conventional approach to characterization, using antibiotic resistance patterns, is often too slow and occasionally unreliable (Achtman 1986), the potential of DNA probe technology was investigated. It was hoped that the use of a panel of DNA probes directed to different parts of the *A. salmonicida* genome might detect alterations at the DNA level in the strains under study. Variations in DNA sequences that occur among individuals of any given species arise from the insertion or deletion of short DNA sequences, or more commonly by single nucleotide changes. These changes may cause variation in

TABLE 1. Seven strains of *Aeromonas salmonicida* were used in the study. The antibiotics and concentrations used were: Tetatetracycline (10 μg); strep = streptomycin (10 μg); Cot = cotrimoxazole (100 μg); Ch = chloramphenicol (25 μg), Fuz = furazolidone (25 μg); Oxo = oxolinic acid (2 μg), Kan = kanamycin (30 μg), Amp = ampicillin (25 μg).

Strain	Antibiotic resistance pattern	Origin
028	Tet^r, $Strep^r$, Cot^r(v)	U.S.A.
DC1	Tet^r, Ch^r, $Strep^r$(v), Cot^r, Fuz^r, Oxo^r, Kan^r, Amp^r.	England – Plymouth
SRT287	Tet^r, Ch^r, $Strep^r$, Cot^r, Fuz^r, Oxo^r, kan^r, Amp^r.	Ireland – Newport
6152	As SRT 287	Ireland – Parteen
030	Drug sensitive[1]	Scotland – Aberdeen
MT004A	Drug sensitive[1], $Strep^r$(v)	Scotland – Aberdeen
MT004	Cot^r	Scotland – Aberdeen

^{r} = resistance.
v = variable resistance.
[1]Drug sensitive = sensitive to all above named drugs.

TABLE 2. DNA probes used in this study.

Plasmid	Probe size and site	Characteristics
TBI/pUC18	H1 insert of 9 kb in EcoR1	Haemolytic on horse blood agar
TB1/pUC18	H2 insert of 2.5 kb in EcoR1	Haemolytic on horse blood agar
1360/pBR322	1360 insert of 1.3 kb in Bam H1	1360 fragment complements an *AroD* gene mutation in *E. coli.*
1321/pUC18	1321 insert of 4.5 kb in Pst 1	1321 fragment complements an *AroA* gene mutation in *E. coli.*

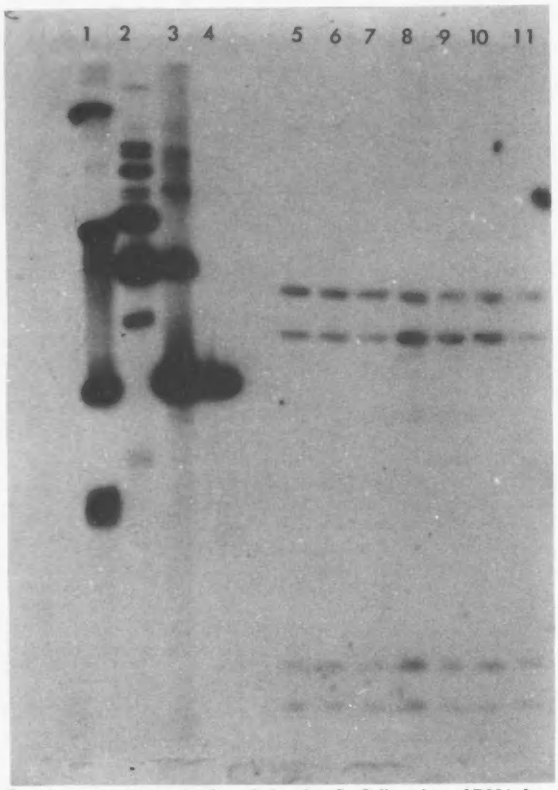

FIG. 1. Autoradiograph of a gel showing SacI digestion of DNA from seven strains of *Aeromonas salmonicida* probed with the 1360 fragment. 1 = pBR322 uncut, 2 = 1360 insert, 3 = 1321 insert, 4 = HI insert, 5 = 6152 SacI, 6 = 028 SacI, 7 = DC1 SacI, 8 = MT004 SacI, 9 = MT004A SacI, 10 = 030 SacI, 11 = SRT287 SacI.

restriction enzyme sites or their spacing which are revealed as variations in the lengths of restriction fragments recognized by a DNA probe when the DNA from different individuals is examined. In this respect seven strains of *A. salmonicida* were analysed.

Materials and Methods

Characterization was dependent on the specific patterns obtained when the genomic DNA from the seven strains (Table 1) was isolated and digested with a restriction enzyme and probed with a DNA probe. Seven restriction enzymes and four different DNA probes were used to obtain a specific pattern for each strain studied.

Southern Blot Analysis

DNA was prepared from the organisms by lysis in sodium dodecyl sulfate (SDS) followed by phenol extractions (Dr. John Neilan, U.C.G., Ireland, pers. comm.). After ethanol precipitation, the DNA was digested with restriction enzyme (Amersham) according to the manufacturer's instructions, electrophoresed on 0.8% agarose gels and transferred to a Nytran filter (S&S). The plasmids carrying the four probes (Table 2) were isolated using caesium chloride centrifugation, and inserts from all but strain H2 were purified using sucrose gradients or electroelution following agarose gel electrophoresis. The DNA was labeled with ^{32}P by nick translation. Hybridization with 1×10^8 counts per min (cpm) of heat denatured probe was at 65°C in 6× sodium saline citrate (SSC) with washes at stringencies up to 0.1 × SSC at 65°C. Following autoradiography for 24–48 h, filters were stripped for rehybridization by boiling in 0.01 × SSPE (20 × SSPE : 3.6 M NaCl, 200 μM NaH_2PO_4 (pH 7.4), 20 μM EDTA (pH 7.4)), 1% SDS for 20 min.

Results and Discussion

DNA from each strain of *Aeromonas* was digested by seven restriction enzymes, Pst 1, Bam H1, EcoR1, Hind 111, Pvu 11, Sac 1, and Taq 1 and electrophoresed overnight on a 0.8% agarose gel. Southern transfer of the DNA to Nytran filters allowed the probing of each filter with four specific DNA fragments. Each probe gave a pattern of bands on each filter and it was expected that if variation between strains occurred at the DNA level then digestion with enzymes and Southern blot analysis of such digestions would lead to identification of a restriction fragment length polymorphism which would permit the identification of individual strains. With the restriction enzymes and probes used in the study no polymorphisms were detected (e.g. Fig. 1). The strains examined were isolated from different locations at different times and were expected to exhibit some variations in the patterns obtained because many exhibit different antibiotic resistances. It remains possible that other combinations of restriction enzymes and probes will uncover a sequence variation in the strains. However, a consideration of the total number of DNA bands revealed in this study (an invariable 131) and the consequent number of nucleotides in the target sites for the restriction enzymes would suggest that the frequency of occurrence of a point mutation is less than 0.08%. The consistancy of the results obtained here contrasts with the estimate of approximately 1% variation in DNA sequences in eucaryotes (Jeffreys 1979).

This present result, coupled with a previous study which showed that the restriction enzyme digestion pattern of plasmids in *A. salmonicida* did not vary over an 8-yr period in which they had grown in the wild (Brazil et al. 1986), attests to the great genetic stability of *A. salmonicida*.

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Effect of Zooplankton Abundance and Body Size on Growth of Age-0 Yellow Perch (*Perca flavescens*) in Oneida Lake, New York, 1975–86[1]

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Mills, E. L., R. Sherman, and D. S. Robson. 1989. Effect of zooplankton abundance and body size on growth of age-0 yellow perch (*Perca flavescens*) in Oneida Lake, New York, 1975–86. Can. J. Fish. Aquat. Sci. 46: 880–886.

We examined an 11-yr (1975–86) field data set to determine whether annual differences in age-0 yellow perch (*Perca flavescens*) growth in weight were related to the abundance, size structure, and species composition of zooplankton in Oneida Lake, New York. A model for prediction of age-0 yellow perch weight was determined using a multiple regression technique; age-0 yellow perch wet weight (grams) was the dependent variable while age-0 yellow perch density, water temperature, calendar day, and cumulative biomass of both zooplankton taxonomic groups (daphnids, "other cladocerans," calanoids, cyclopoids, and nauplii) and zooplankton size classes (<1.1 mm, 1.1–1.7 mm, and >1.7 mm) were the independent variables. Analyses were based on an integrated approach where time was measured in cumulative temperature units and yellow perch weight was considered a function of the cumulative amount of food available. Below a cumulative temperature of 1350 °C·d^{-1}, none of the independent variables were related significantly (P <0.05) to yellow perch weight. Beyond 1350 °C·d^{-1}, age-0 yellow perch weight was strongly correlated with the biomass of *Daphnia* and significant (P <0.05) prey size variables shifted toward larger prey as fish grew. Our results indicate size- and species-based interactions between fish and zooplankton play an important role in regulating growth of age-0 fish.

Nous avons examiné des données recueillies sur le terrain pendant 11-an (de 1975–86) pour déterminer si les différences annuelles de poids de la perchaude (*Perca flavescens*) d'âge 0 est reliée à l'abondance, à la taille et aux espèces du zooplancton du lac Oneida (New York). On a élaboré un modèle permettant de prédire le poids des perchaudes d'âge 0 à l'aide d'une technique de régression multiple; le poids frais (grams) de la perchaude d'âge 0 était la variable dépendante et la densité de la perchaude d'âge 0, la température de l'eau, la journée et la biomasse cumulative des groupes taxinomiques de zooplancton (daphnies, "autres cladocères," calanoïdes, cyclopoïdes et nauplius) de même que les catégories de tailles de zooplancton (<1,1 mm, 1,1–1,7 mm et >1,7 mm) étaient les variables indépendantes. Les analyses étaient fondées sur une approche intégrée suivant laquelle le temps était mesuré en unités cumulatives de température et le poids de la perchaude était considéré comme une fonction de la quantité cumulative de nourriture disponible. En dessous d'une température cumulative de 1350 °C·d^{-1}, il n'y avait aucune corrélation significative (P <0,05) entre les variables indépendantes et le poids des perchaudes. Au dessus de 1350 °C·d^{-1}, le poids des perchaudes d'âge 0 était étroitement corrélé à la biomasse des daphnies et la grosseur des proies augmentait de façon significative (P <0,05) avec la croissance des poissons. Nos résultats montrent que les interactions où interviennent la taille et l'espèce entre les poissons et le zooplancton jouent un rôle important dans la régulation de la croissance des poissons d'âge 0.

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Young-of-the-year fish in freshwater lake ecosystems are important as both food for larger fish and as consumers of zooplankton. Fluctuations in the abundance of these fish can affect growth and recruitment of piscivorous predators (Forney 1974), impact the size structure and species composition of the zooplankton community (Mills and Forney 1983; Mills and Forney 1988; Crowder et al. 1987), and indirectly influence the abundance and composition of the algal community through predation effects on zooplankton (Mills et al. 1987). Zooplankton-mediated alteration of algal biomass and composition can affect nutrients, extending the impact of predation throughout the trophic hierarchy (Mills et al. 1987). Depending on cohort strength, age-0 fish can impact all trophic levels of aquatic ecosystems.

Young planktivorous fish are size selective predators (Siefert 1972; Hansen and Wahl 1981) and generally select prey smaller than they are capable of eating (Hansen and Wahl 1981; Mills et al. 1984). There is much information describing the diet of age-0 fish (Noble 1975; Guma'a 1978; Keast 1980; Teska and Behmer 1981; Mathias and Li 1982) and the relationship

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between growth of young fish and food supply has been observed (Noble 1975; Lemly and Dimmick 1982). However, little is known about the interaction between prey selectivity and growth of age-0 fish. For young planktivorous fish which prefer certain prey species (Noble 1975; Mills et al. 1984) and feed selectively on small to intermediate size prey, a logical question is: what roles do body size and prey species play in regulating first-year growth? In this study, we hypothesized that age-0 yellow perch growth is related to species composition and body size of zooplankton. To test this hypothesis, we examined an 11-yr (1975–86) field data set and determined, using a multiple regression techique, whether differences in yellow perch (*Perca flavescens*) growth in weight were related to abundance, size structure, and species composition of zooplankton in Oneida Lake, New York.

Background

Oneida is a shallow eutrophic lake (mean depth = 6.8 m) covering 20 700 ha on the Ontario Lake Plain of central New York. The walleye (*Stizostedion vitreum vitreum*) is the dominant piscivorous fish and age-0 yellow perch along with white perch (*Morone americana*) and gizzard shad (*Dorosoma cepedianum*), are the main link in the transfer of energy from secondary to higher trophic levels. Because cohorts of age-0 fish vary in initial size and are subject to different rates of predation, the biomass of these planktivores fluctuates both seasonally and annually (Mills and Forney 1988).

In Oneida Lake, age-0 yellow perch are important as predator and prey. Young yellow perch are usually the most abundant prey species observed in walleye stomachs. Annual growth and production by walleye have been closely tied to first-year yellow perch production (Forney 1974). Age-0 yellow perch also prey upon daphnids and consistently collapse the *Daphnia pulex* population when biomass of these fish exceeds 20 $kg \cdot ha^{-1}$ (Mills et al. 1987). When *Daphnia pulex* disappears, there is a shift in the size structure and species composition of the zooplankton to smaller cladocerans and the mean size of the crustacean community declines. Although yellow perch can subsist on these smaller zooplankters, their growth is substantially reduced (Mills and Forney 1981).

Methods

Field Data

Concurrent data on age-0 yellow perch weight, zooplankton body size and composition, and temperature were collected from two sites in Oneida Lake at approximately weekly intervals from late July through October, 1975–86. There was no data on zooplankton body size available for 1978. The sites are similar in depth. Although they are 10 km apart, they are not considered isolated for two reasons: (1) the lake is usually homothermal; average water column temperature differences between sites rarely exceed 1°C and (2) the distribution of zooplankton is spatially unpredictable because of wind and currents (Powell 1979). For these reasons, site specific differences that might influence fish and zooplankton distribution in some lakes were not a concern in this study. Consequently, data on age-0 yellow perch and zooplankton were pooled from both study sites in regression analyses.

Weekly changes in age-0 yellow perch growth in weight (grams) were determined using bottom trawls; fish were collected with a 5.9-m otter trawl (13-mm stretch mesh cod end) towed for 5 min at approximately weekly intervals from late July through October at each site. Total lengths and wet weights of age-0 yellow perch were recorded from each trawl catch. Growth, the addition of weight with time, was estimated from weighted means of several hundred to several thousand young yellow perch.

TABLE 1. List of zooplankton species found in Oneida Lake, New York between 1975 and 1986. Zooplankton species are numbered to which group they belong; 1 = daphnids; 2 = other cladocerans; 3 = calanoids; 4 = cyclopoids.

Cladocera
Bosminidae
Bosmina longirostris (2)
Eubosmina coregoni (2)
Sididae
Diaphanosoma leuchtenbergianum (2)
Daphnidae
Daphnia galeata mendotae (1)
D. pulex (1)
Ceriodaphnia quadrilangulata (2)
Chydoridae
Chydorus sphaericus (2)
Copepoda: Calanoida
Temporidae
Epischura lacustris (3)
Diaptomidae
Diaptomus minutus (3)
D. oregonensis (3)
Copepoda: Cyclopoida
Cyclopoidae
Cyclops bicuspidatus thomasi (4)
Mesocyclops edax (4)

Concurrent zooplankton samples were also collected weekly; abundance, composition, and body size of zooplankton were determined from vertical hauls with a 0.5-diameter 153-μm-mesh net. Zooplankton were preserved in either 100% isopropyl alcohol or a sucrose-4%-formalin solution. Counts and lengths were recorded using an overhead microscope projector with electronic calipers interfaced with an Apple microcomputer (Mills and Confer 1986). Zooplankton were identified to species and were measured from the anterior margin of the head to the base of either the tail spine of cladocerans or the caudal rami of copepods. Biomass, density, average length, and average weight of each zooplankton species were recorded for each sample. Weekly temperature (degrees celsius) was measured at 1-m intervals surface to bottom and averaged over the entire water column.

Zooplankton were divided into groups according to either species or size. The species groups, made up of species observed to co-occur regularly in the seasonal succession of Oneida Lake (Mills et al. 1987) were (1) daphnids, (2) other cladocerans, which predominate when the daphnid population collapses, (3) calanoids, which are abundant in spring and early summer, (4) cyclopoids, and (5) nauplii of all copepod species. Table 1 indicates which species belong to each group. The size groups were small (<1.1 mm), medium (1.1–1.7 mm), and large (>1.7 mm).

Density of age-0 yellow perch was estimated from the catch and volume strained by high speed samplers (Noble 1970). After young switched to a demersal mode in July, trawls were fished at weekly intervals through mid-October and cohort abundance was approximated from the catch and area swept (Forney 1971). Over the 11-yr study period, weekly lakewide density estimates

were made from bottom trawls at 10 to 17 different sites. The lakewide estimates were employed in our analysis as the best available measures of yellow perch density.

Growth, Temperature, and Zooplankton Abundance

Temperature, as well as food abundance, influences fish growth (Brett 1979). Rather than introduce temperature as another explanatory variable, which might swamp the effects of zooplankton abundance and prey body size on growth, we chose to measure time in units that take lake water temperature into account: degree-days above 0°C (degrees celsius per day), starting from the time when the larvae reached 18 mm (because neither spawning nor hatching time were known for all years) (referred to as temperature days hereafter). Lake water temperature was accumulated on a daily basis (based on linear interpolation between weekly observations) and fish growth was compared with prey abundance across years on specific temperature days.

The most direct approach to measuring fish growth in the field would be weight change in a week as a function of food during the week; but differences between starting and ending weights are very sensitive to measurement errors, and feeding on zooplankton may not be converted immediately to growth. We therefore took an integrated approach and considered total fish weight as a function of the cumulative amount of zooplankton available from when yellow perch were 18 mm to a specific date, corrected for temperature and expressed as grams per litre per degree celsius per day.

Data Analysis

To predict age-0 yellow perch weight, we used a stepwise multiple regression model (Helwig and Council 1982) and included the variables in the form

$$\text{Age-0 yellow perch weight (grams)} = a + b_1(X_1) + b_2(X_2) + \ldots . b_n(X_n),$$

where a is the intercept, b_1, b_2 etc. are constants, and X_1, X_2, $\ldots . X_n$ represent yellow perch density (number per hectare), temperature (degrees celsius), calendar day, and the cumulative biomass (grams per litre per degree celsius per day) either of each zooplankton species group or of each zooplankton size group. These variables were added in order of significance to the regression model. Age-0 yellow perch density was included in the model because density can indirectly influence yellow perch growth (Mills and Forney 1981); temperature was included since cumulative temperature may not completely account for temperature effects on growth; calendar day was included because the day a given cumulative temperature is reached varies between years, and zooplankton biomass represented the cumulative amount of food available on a specific temperature day. All years were included in the regression analysis; separate regressions were run using either the cumulative biomass of individual zooplankton species or size class groups. Regressions were run at temperature days of 750, 950, 1150, 1350, 1550, 1750, 1950, 2150, and 2350 °C·d^{-1} (late June to mid-October). Only those variables that contributed significantly ($P < 0.05$) to a reduction in unexplained variance in yellow perch weight were included in the two regression models.

Results

Temperature

Water temperature, averaged for the two Oneida Lake sites for each year, varied by as much as 5.4°C on August 1 between

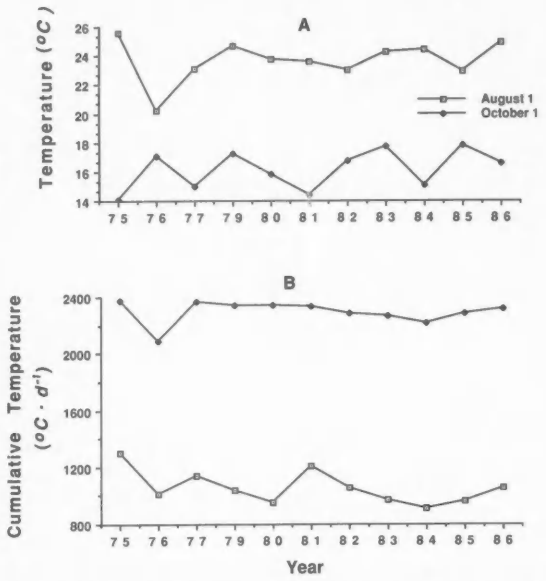

FIG. 1. Trends in Oneida Lake water temperature (A) and cumulative water temperature (B) on August 1 and October 1, 1975–86.

TABLE 2. Density, biomass, and wet weight of age-0 yellow perch in Oneida Lake on August 1 and October 1, 1975–86. Wet weights were determined from the catch of fish in bottom trawls and fish abundance was determined from the catch and area swept by bottom trawls.

Year	Age-0 Yellow Perch		
	Density (No.·ha^{-1})	Biomass (kg·ha^{-1})	Weight (g)
	August 1		
1975	27 380	23.4	1.63
1976	6500	9.4	1.55
1977	15 680	28.9	2.27
1979	13 400	17.4	0.66
1980	8900	14.3	1.05
1981	21 172	16.1	0.78
1982	16 120	11.5	0.91
1983	9623	15.9	1.65
1984	5030	7.3	1.53
1985	8390	13.7	1.42
1986	509	1.2	1.81
	October 1		
1975	1190	3.0	2.91
1976	458	1.9	5.03
1977	5510	18.4	3.41
1979	710	3.3	4.20
1980	2504	0.3	5.25
1981	4173	9.2	2.24
1982	1472	3.8	2.75
1983	1079	5.6	4.63
1984	1237	4.5	3.39
1985	3401	12.1	3.75
1986	103	0.6	6.48

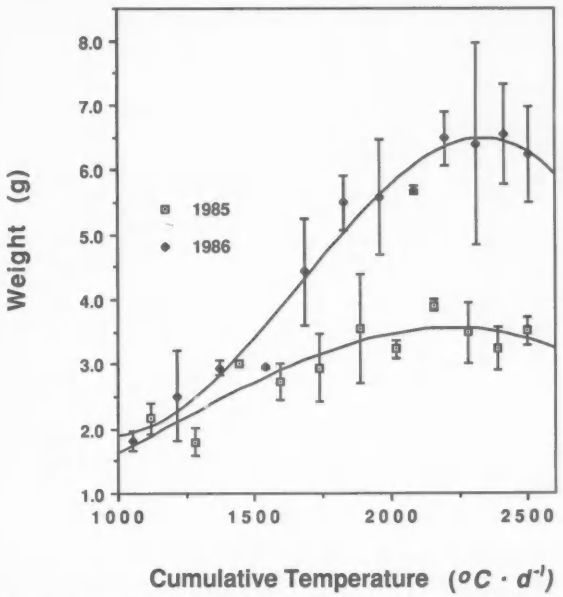

FIG. 2. Comparison of age-0 yellow perch growth in weight determined from fish caught in bottom trawls in Oneida Lake at cumulative water temperatures between 1000 and 2500 °C·d^{-1}, 1985 and 1986.

1975 and 1986; by October 1, water temperature declined and varied by as much as 3.1°C between years (Fig. 1A). The cumulative temperature on August 1 for all years ranged between 888 and 1267 °C·d^{-1} and on October 1 ranged between 2091 and 2369 °C·d^{-1}, a shift in the calendar date by as much as 2 wk for a specific cumulative temperature (Fig. 1B). More specifically, August 1, 1975 had a cumulative temperature of 1297 °C·d^{-1}, the same as August 14, 1983. Thus, to correct yellow perch growth for temperature effects, the weight of yellow perch on August 1, 1975 was compared with the weight of those fish on August 14, 1983. By October, however, cumulative temperature was less variable and centered around 2300 °C·d^{-1}; the only exception was 1976 when the cumulative temperature on October 1 was 2091 °C·d^{-1}.

Yellow Perch Abundance and Growth

Large annual fluctuations in age-0 yellow perch density occurred between 1975 and 1986; greater than 50-fold differences in year-class size and greater than 60-fold differences in biomass existed by a cumulative temperature date corresponding to October 1, indicating that early survival of age-0 yellow perch was highly variable (Table 2). For all years, mean yellow perch abundance decreased by 84% and mean biomass decreased by 60% from August 1 to October 1.

Mean weights of young yellow perch collected at weekly intervals increased steadily with cumulative water temperature but maximum weight by 2500 °C·d^{-1} was variable (Fig. 2). For example, young yellow perch averaged 3.24 g at 2500 °C·d^{-1} in 1985 and 6.55 g on the same temperature day in 1986. Over the 11-yr study period, weight of yellow perch at 2500 °C·d^{-1} differed by nearly three times and mean wet weights ranged between 1.27 and 6.55 g.

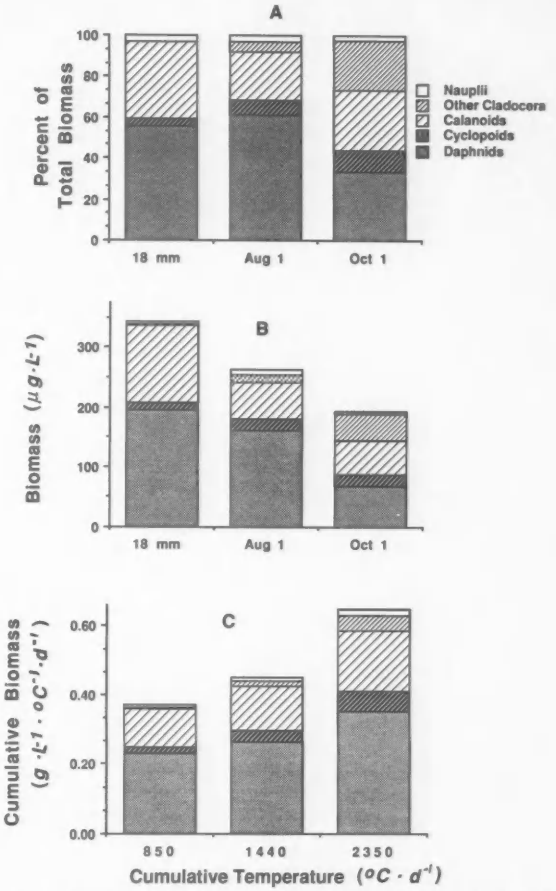

FIG. 3. Percent of total biomass (A) and seasonal biomass (B) when age-0 yellow reached 18 mm and on August 1 and October 1, and cumulative biomass (C) of zooplankton species groups on specific temperature days in Oneida Lake averaged for all years between 1975 and 1986.

Zooplankton Composition and Abundance

Mean biomass of the five zooplankton species groups were compared on temperature days of 850, 1440, and 2350 °C·d^{-1} for all years between 1975 and 1986; these temperature days corresponded to dates of mid-July, mid-August, and early October, respectively (Fig. 3C). Total zooplankton biomass increased between 850 and 2350 °C·d^{-1}; the cumulative biomass was greatest for the daphnids and calanoid copepods and lowest for nauplii. The average biomass of zooplankton species groups from when age-0 yellow perch reached 18 mm to October 1 was dominated by daphnids; calanoids and cyclopoids increased from 30 to 42% of the total biomass and the biomass of other cladocerans expanded from 0.3 to 25% of the total biomass over the same time period (Fig. 3A and 3B). As might be expected, annual variation in the biomass of the zooplankton groups was considerable; greatest annual variation in seasonal biomass was evident for *Daphnia* which by 2350 °C·d^{-1} ranged from 0 to 315 μg·L^{-1}.

The biomasses of small, medium, and large sized zooplankton were also averaged over all years between 1975 and 1986

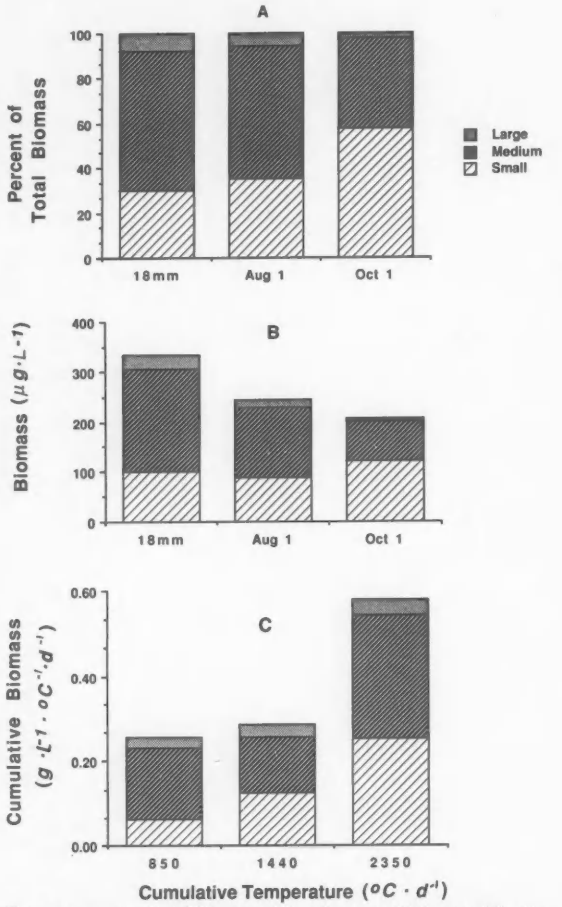

FIG. 4. Percent of total biomass (A) and seasonal biomass (B) when age-0 yellow perch reached 18 mm and on August 1 and October 1, and cumulative biomass (C) of small (<1.1 mm), medium (1.1–1.7 mm), and large (>1.7 mm) zooplankton on specific temperature days in Oneida Lake averaged for all years between 1975 and 1986.

on three temperature days. Cumulative biomass of medium-sized zooplankton was greater than either the small or large zooplankton on 850 °C·d^{-1} (Fig. 4C). By 2350 °C·d^{-1}, the cumulative biomass of medium zooplankton continued to dominate although the biomass of the small zooplankton size category increased substantially between 850 and 2350 °C·d^{-1}. Seasonally, the biomass of all zooplankton in the medium size category decreased while the biomass of small sized zooplankton increased from when age-0 yellow perch were 18 mm through October (Fig. 4A and 4B).

Regression Analysis

To test if age-0 yellow perch growth was related to zooplankton species composition, the cumulative biomass of five species groups were included in the regression model. Other variables in the regression model included yellow perch density, temperature, and calendar day. Below a cumulative temperature of 1350 °C·d^{-1} (Table 3), none of the variables contributed significantly ($P > 0.05$) to the prediction of total yellow perch weight. Above 1350 °C·d^{-1}, corresponding to the calendar time of early to mid-August through October, cumulative biomass of *Daphnia* contributed significantly ($P < 0.05$) to a reduction in unexplained variance in age-0 yellow perch weight and was always the first variable added in the stepwise regression. Coefficients were positive for *Daphnia*, indicating that age-0 yellow perch weight increased proportionately with cumulative biomass of *Daphnia*. Besides *Daphnia*, the independent variable "cyclopoids," and "other cladocerans" also contributed to the total variance (5–7%) at 1550 °C·d^{-1} and "other cladocerans" contributed 19% of the total variance at 2150 °C·d^{-1}. The percentage of the variance in yellow perch weight explained by the cumulative biomass of zooplankton groups and the other five variables in the regression (R^2) ranged between 40 and 78%.

To test if prey body size correlates with fish weight as fish grow, the cumulative biomass of small, medium, and large zooplankton were included along with the variables yellow perch density, temperature, and calendar day in the regression model. None of the variables contributed significantly ($P > 0.05$) to the prediction of yellow perch weight below a cumulative temperature of 1350 °C·d^{-1} (Table 3). Above 1350 °C·d^{-1}, yellow perch density was not a significant ($P > 0.05$) correlate of yellow perch weight but significant relationships were evident between zooplankton body size and yellow perch weight as these fish grew. When the cumulative temperature was 1350 °C·d^{-1}, cumulative biomass of small and medium zooplankton contributed significantly ($P < 0.05$) to the explained variance in fish weight. Between 1550 and 1750 °C·d^{-1}, medium sized zooplankton was the most significant ($P < 0.05$) correlate of yellow perch weight, and beyond a cumulative temperature of 1950 °C·d^{-1}, the cumulative biomass of large sized prey became the most significant ($P < 0.05$) variable in the prediction of yellow perch weight. In addition, the cumulative biomass of medium sized prey beyond 1950 °C·d^{-1} was the second most significant variable ($P < 0.20$), reducing the unexplained variance by 8–12%. Coefficients of significant variables were positive and all six independent variables in the regression model (R^2) explained 48–69% of the variance in yellow perch weight.

Discussion

A time reference based on temperature is a potentially useful approach to comparing fish growth over several years. In this study, we chose temperature day instead of calendar day as our standard time reference since fish weight achieved on a specific temperature day represented a shift in calendar day by as much as two weeks. Temperature is a critical determinant of fish growth (Brett 1979) and, therefore, the use of temperature day as a standard unit of measure reduces the swamping effect temperature could have on other factors influencing fish growth. In addition to standardizing time, we also took an integrative approach and considered total fish weight as a function of the cumulative amount of food available to a specific temperature day. This is the only study that we are aware of where both cumulative units of temperature and food resources have been applied to analyzing fish growth. Finally, the standardizing of time and indexing of cumulative food resources does have direct application to other studies of food and growth, particularly for those organisms whose growth is sensitive to temperature.

Young planktivorous fish show a high degree of selectivity based on zooplankton body size (Feller and Kaczynski 1975; Furnass 1979; Mathias and Li 1982), and generally select small- to intermediate-sized prey (Hansen and Wahl 1981), even

TABLE 3. Coefficients to predict age-0 yellow perch weight (g) from yellow perch (YP) density (No.·ha^{-1}), water temperature (°C), calendar day, cumulative biomass (g·L^{-1}·°C·d^{-1}) of zooplankton species groups (*Daphnia*, calanoids, cyclopoids, other cladocerans, and nauplii), and cumulative biomass (g·L^{-1}·°C·d^{-1}) of zooplankton size groups (small, medium, and large) on nine different temperature days using stepwise regressions. Order of addition of variables in stepwise regression is shown. Nonsignificant variables ($P > 0.05$) were excluded.

Daily cumulative temperature (°C·d^{-1})	Independent variables								Intercept	R^2
	Age-0 YP	Water temp.	Calendar day	*Daphnia*	Calanoids	Cyclopoids	Other cladocerans	Nauplii		
				Zooplankton species groups						
750 950 1150										
1350				2.71					−0.248	0.40
1550				4.04		19.04	21.05		−3.877	0.77
				(1)		(2)	(3)			
1750				4.26					1.405	0.60
1950				5.81					0.774	0.59
2150				5.58			−27.54		4.042	0.76
				(1)			(2)			
2350				5.69					5.617	0.78
				Zooplankton size groups						
	Age-0 YP	Water temp.	Calendar day	Small	Medium	Large			Intercept	R^2
750 950										
1150										
1350				8.26	3.35				−2.035	0.52
				(1)	(2)					
1550					3.05				−3.448	0.60
1750					5.05				−1.728	0.48
1950						20.34			1.666	0.54
2150						17.78			2.237	0.64
2350						22.85			5.057	0.69

though they can ingest larger-sized prey (Mills et al. 1984). Size selectivity implies a mechanism for optimizing foraging efficiency to maximize assimilatable energy directed toward increasing body length, weight, or condition. Consequently, growth and prey selectivity by age-0 fish should be closely linked although the notion that prey size and growth are interrelated has only been tested for Atlantic salmon, *Salmo salar* (Wankowski and Thorpe 1979). Results of this study indicate that zooplankton species composition and body size play a role in regulating growth of age-0 yellow perch. Cumulative biomass of *Daphnia* contributed significantly to the prediction of yellow perch weight and agreed with earlier studies that showed young yellow perch selected *Daphnia* over other zooplankton species (Noble 1975). Zooplankton body size was also an important factor in predicting fish weight and shifted from small to medium to large zooplankton as age-0 yellow perch grew. Studies of prey selectivity by Hansen and Wahl (1981) and Mills et al. (1984) have also shown that age-0 yellow perch shift toward increasingly larger prey as fish size increases. Results from our regression analyses reflect the dependence of age-0 yellow perch weight on *Daphnia* and zooplankton body size (Table 3) and support the idea that prey selectivity and growth of these fish are interrelated.

Earlier studies have shown that yellow perch density is a critical factor influencing yellow perch growth and *Daphnia* abundance; when yellow perch density was high, growth was slow, and *Daphnia* were scarce (Mills and Forney 1981). In our regression analyses, yellow perch density was included as an independent variable, and in all cases, this variable was not strongly correlated with yellow perch growth. Instead, a stronger correlation occurred between fish weight and zooplankton composition (e.g. *Daphnia*). Such results are expected if the indirect effects of yellow perch growth are expressed through changes induced in the structure of the food web and are consistent with the idea that a high density of yellow perch in early summer triggers a shift in the zooplankton community and subsequent growth is not strongly influenced by age-0 yellow perch density but by zooplankton composition (Mills and Forney 1981). More specifically, if *Daphnia* density directly affects yellow perch growth, and if yellow perch density only indirectly affects yellow perch growth through its effect on *Daphnia* biomass, then *Daphnia* biomass would be expected to be more strongly correlated with age-0 yellow perch growth.

Our inability to detect a significant relationship between age-0 yellow perch weight and zooplankton biomass prior to an accumulative temperature of 1350 °C·d^{-1} (before August 1) is interesting. We suspect this lack of correlation is related to the seasonal growth pattern of yellow perch cohorts and community changes in the zooplankton population. Yellow perch cohorts generally reach their maximum biomass in July and early August, and if the cohort reaches a density of 20–40 kg·ha^{-1}, the *Daphnia pulex* population will collapse (Mills and Forney 1983). If yellow perch collapse the *Daphnia* population, these fish are forced to seek alternate prey, and growth declines (Mills and Forney 1981). Consequently, prior to the collapse of *Daphnia pulex* and before 1350 °C·d^{-1}, the composition and abundance of zooplankton are less variable and food resources are likely not limiting so that large differences in yellow perch

growth are not apparent. By fall, however, growth patterns in yellow perch cohorts diverge and linkages between yellow perch total weight and variability in *Daphnia* abundance become more evident.

For adult planktivorous fish, an interrelationship between prey body size, predator body size, and growth efficiency has been demonstrated (Paloheimo and Dickie 1965, 1966a,b; Kerr 1971a,b). In effect, the net energy gained by large fish eating large prey outweighs the possible disadvantages associated with capture and ingestion. In contrast, the effects of particle size and food type on growth have not been adequately evaluated for young planktivores. As noted previously, the only suggestion that prey size influences growth of age-0 fish is shown for juvenile Atlantic salmon (*Salmo salar*) (Wankowski and Thorpe 1979). For these fish, growth rates were closely related to particle size, and the optimum prey size for maximum growth rate increased with fish length. Our regression analyses indicated a switch in prey (1.1–1.7 mm) to large prey (>1.7 mm) when these fish ranged from 60 to 75 mm total length. The switch from medium to large zooplankton body size was compatible with the findings of Hansen and Wahl (1981) who predicted young yellow perch would select 1.7-mm prey at about 66 mm total length. Large prey was the most significant variable influencing yellow perch growth beyond 1950 $°C \cdot d^{-1}$, medium sized prey was always the first or second most significant variable influencing growth of these fish between 1350 and 2350 $°C \cdot d^{-1}$. Consistent with this information are findings from our own recent laboratory work that shows young yellow perch achieve a higher total weight when fed medium (1.1–1.7 mm) compared with larger and smaller *Daphnia*. Consequently, the shift toward larger prey with increasing fish weight and the importance of medium size prey suggest a linkage between prey size and growth and indicate that the factor of prey size should be considered in studies involving growth of young planktivorous fish.

Food availability is especially critical to growth and survival of fish during their first year of life. Our results suggest that the availability of *Daphnia* and the availability of suitably sized zooplankton in Oneida Lake is important to age-0 fish growth. In years when growth of the yellow perch cohort is slow, the period of vulnerability to predation is prolonged and survival is low (Forney 1980). Alternatively, in years when age-0 yellow perch growth is rapid, daphnids are abundant and survival of these fish is high. Consequently, interrelationships between zooplankton abundance, prey selection, and first-year growth have direct impact on our basic understanding of the mechanisms underlying recruitment variability in fish populations.

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Survival of Atlantic Halibut (*Hippoglossus hippoglossus*) Caught by Longline and Otter Trawl Gear

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To assess the effectiveness of a proposed minimum size limit (81 cm) for Atlantic halibut (*Hippoglossus hippoglossus*) in Canadian waters, the survival of small fish caught in longline and bottom trawl gear was examined using live holding facilities onboard a research vessel and subsequently, in a land-based laboratory. Commercial practices were simulated during fishing operations. Of halibut less than the proposed size limit, 35% of the otter trawl catch and 77% of the longline catch survived more than 48 h. Factors potentially influencing halibut survival (handling time, total catch, fish length, maximum depth fished, and trawl duration) were examined using proportional hazard models. On the basis of those analyses, it was concluded that in bottom trawl sets of duration used in the commercial fishery (≥2 h), higher survival times were associated with shorter handling time, larger fish size, and comparatively small total catch weight. Supplemental information on the condition of trawl-caught halibut was also obtained from observers stationed onboard commercial trawlers.

Afin d'évaluer l'efficacité d'une taille minimale (81 cm) proposée pour le flétan de l'Atlantique (*Hippoglossus hippoglossus*) vivant dans les eaux canadiennes, on a examiné la survie des petits poissons pêchés à la palangre et au chalut de fond, au moyen de viviers placés à bord d'un navire de recherches puis dans un laboratoire situé à terre. On a simulé des pratiques commerciales durant les opérations de pêche. Chez les flétans dont la taille était inférieure à la taille minimale proposée, 35 % des poissons pêchés au chalut à panneaux et 77 % des poissons pêchés à la palangre ont survécu plus de 48 h. On a examiné les facteurs pouvant influer sur la survie des flétans (temps de manoeuvre, pêche totale, longueur des poissons, profondeur maximale de la pêche, et durée du chalutage) en utilisant des modèles aléatoires proportionnels. Ces analyses ont permis de conclure que, dans les séries de chalutage de fond d'une durée comparable à celle employée dans la pêche commerciale (sup. ou égale à 2 h), il a été possible de relier les temps de survie les plus longs aux temps de manoeuvre les plus courts, à la plus grande taille de poissons et à un poids total de pêche comparativement petit. Des observateurs postés à bord de chalutiers commerciaux ont pu fournir des données supplémentaires sur l'état des flétans pêchés au chalut.

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The Atlantic halibut (*Hippoglossus hippoglossus*) fishery off Canada's east coast is growing in significance due to increased landings and value. Landings of Atlantic halibut in 1986 were 3555 t, with the Scotian Shelf, Gulf of St. Lawrence, and Newfoundland/Labrador regions contributing 45, 8, and 47%, respectively. The landed value of the catch in 1986 was $14,870,000. While longline gear is responsible for the bulk of Scotian Shelf and Gulf of St. Lawrence landings, trawl catches off Newfoundland comprise almost as large a fraction of landings as do longline catches. In the most northerly region (NAFO Subarea 2 + 3KL), the trawl catch is greater than that of the longline component of the fishery.

There are several management initiatives currently under development, including a minimum retained fish length of 81 cm. From a conservation perspective, such a measure can only be effective if an acceptable proportion of fish returned to the water survive capture, handling, and release. Possible sources of mortality include depressurization (Feathers and Knable 1983), injuries incurred while hooked (Peltonen 1969; Dotson 1982), and muscular fatigue (Parker et al. 1959; Beamish 1966). The extent of such mortality can be determined using live tanks (Peltonen 1969), through tag recoveries, qualitative assessment by observers onboard the fishing vessels (Hoag 1975), and by acoustic telemetry (Jolley and Irby 1979). Once information on survival rates is obtained, the data can be incorporated into the Beverton and Holt yield per recruit model, thus allowing the impact of a minimum fish size on yield to the fishery to be determined (Waters and Huntsman 1986).

On the basis of tag returns, Hoag (1975) inferred a survival rate of about 50% for trawl-caught and released Pacific halibut

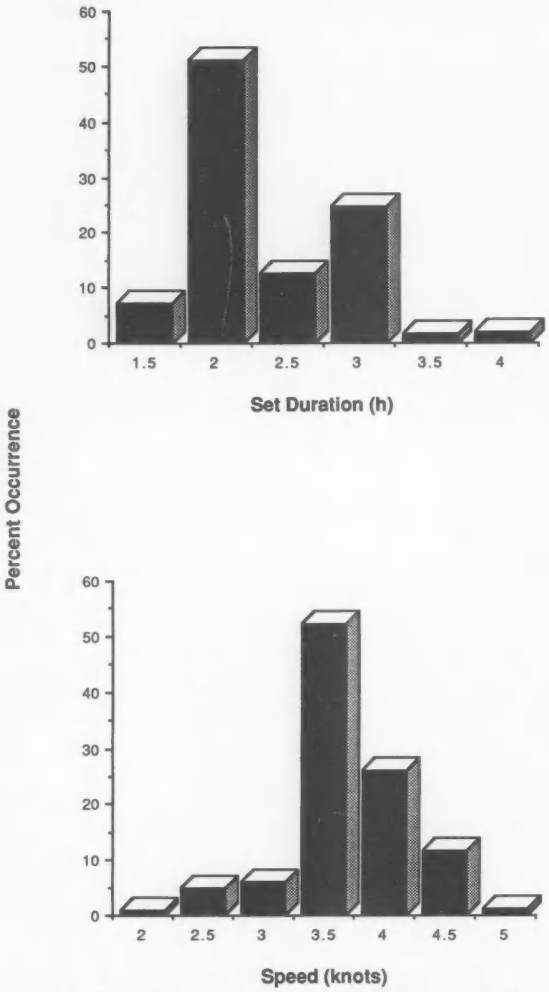

FIG. 1. Distributions of tow speeds and set durations recorded by staff of the International Observer Program in sets where halibut were caught, NAFO Subareas 3 and 4, 1981–87, $N=981$. Thirteen sets were greater than 4-h duration, and 40 sets were made at speeds greater than 5 knots.

(*Hippoglossus stenolepis*) less than 80 cm. In examining factors which influenced survival, Hoag found a positive correlation with fish length and a negative correlation with time on deck and the weight of the total catch. The technique assumes that the probability of a recaptured fish being reported is the same regardless of size and that mortality due to capture occurs shortly after release. In our case, we chose not to employ tag returns as a means of estimating survival, due to potential problems in partitioning mortality associated with previous capture and release from fishing mortality, which is currently unknown. A further complication with the method is obtaining estimates of the extent of nonreporting of captures of tagged fish. However, Hoag's study is particularly noteworthy in the context of this paper, as some investigators feel that Pacific and Atlantic halibut are conspecific (Bell 1981).

In this paper, we report results on halibut survival from experimental fishing employing both an otter trawl and longlines, the two major gear components in the east coast Atlantic halibut fishery. Using holding tanks for observations of fish caught during the experimental fishing, we assessed the probability of survival and factors influencing mortality in both longline and trawl-caught fish. The statistical models employed were of the proportional hazard type, as commonly used in engineering and biomedical applications (Lawless 1982), but novel for fisheries science. The advantage of modeling hazard functions and survival times is that results can be expressed in terms of percentiles of a distribution, which would then permit the prediction of the percent surviving past a certain critical time, for instance. Ancillary observations on the condition of trawl-caught halibut were also collected onboard commercial fishery vessels. Such data allowed us to assess whether the fishing and processing operations onboard the research vessel realistically simulated commercial fishery practices. The analysis presented here comprises the first step towards assessing the impact of a minimum size regulation on the east coast halibut fishery.

Methods

Data Obtained using a Research Vessel

Experimental fishing for Atlantic halibut was conducted onboard the 58-m research trawler RV *Lady Hammond* on the slopes of Sable Island Gully (43°56′N, 58°58′W), from June 29 to July 7, 1987. The otter trawl employed was the Western IIA, the standard trawl used in surveys of groundfish abundance on the Scotian Shelf conducted annually by the Department of Fisheries and Oceans (Halliday and Koeller 1981). Typically, bottom trawls currently employed in the commercial fishery are somewhat larger in overall dimension and have larger mesh in the codend. Hence, to better simulate commercial fishing gear, we removed the 20-mm codend liner. On the basis of examination of data provided by observers stationed onboard commercial fishery trawlers (International Observer Program), we concluded that set duration should be 2 h, and that the speed of the trawl over the bottom should be 3.5–4 knots (Fig. 1). However, during the course of experimental fishing, some shorter sets were completed for the purpose of collecting halibut in good condition for other experiments in the laboratory, and to allow us to compare the effect of shorter set duration on halibut survival.

Once the otter trawl set was completed, bridge personnel were asked to record when the codend was on the deck. The catch was then sorted, and undersized (<81 cm) halibut set aside. Several larger halibut were also kept to meet other program objectives, and those data are also included in the analyses. In our attempt to follow commercial fishing practices, halibut often remained in the sorting bin for an extended period prior to being placed in the holding tanks. In that fashion, we obtained a reasonably wide range of values for handling time. Each halibut was measured and tagged (if alive and to be retained) with an individually numbered anchor tag (Floy Tag Manufacturing, Seattle, WA, Type FD68B) and the time when fish were placed in a holding tank noted. With the knowledge of when the codend was on deck and when fish were placed in the tank, the total time out of water was then calculated for each individual. The total catch weight for all species was also estimated for each set.

To allow us to qualitatively describe the type of external injury associated with capture in the two gear types, we

designed a form which included a drawing of both the pigmented and unpigmented side of the fish. Once a fish died, the location of any injuries was noted on the form and assigned a code, as follows: 1 — slight damage, including scratching; 2 — scale loss; 3 — redness, bruising; 4 — open wounds with musculature clearly visible; 5 — damaged jaws.

The longline gear employed was of a type currently used in the fishery, and included 16/0 circle hooks, 152-cm long gangions and stainless steel snaps. The spacing between gangions was about 5 m. To ensure that commercial fishing practices were adhered to, a fisherman familiar with halibut longlining techniques was contracted to be in charge of that aspect of fishing operations. Handling time was kept to a minimum since during normal fishing operations, fish to be returned to the water would be released immediately. In subsequent analyses, handling time for the longline-caught fish was treated as a constant. As was the case for trawl-caught halibut, the fish which were retained were measured and tagged with an individually numbered anchor tag.

The onboard holding facility was a modification of that fully described by Waiwood (1988), except that two of the original three holding tanks were replaced by two 2 × 1 × 1.5-m high tanks, thereby doubling the holding capacity. A refrigeration unit maintained temperature at the then current bottom temperature (7° ± 1°C), as determined by a XBT cast. Water was recycled through sand and charcoal filters with an 8% (5 $L \cdot min^{-1}$) rate of replacement with ambient water. The water was aerated, and dissolved oxygen levels measured regularly. In a few instances when the dissolved oxygen level fell below 7 $mg \cdot L^{-1}$, it was immediately restored by bubbling medical grade oxygen into the tanks. Upon completion of the cruise, the fish were transferred to similar holding tanks at the Biological Station, St. Andrews, for the completion of the 50-d long experiment. While detailed observations were made for 50 d only, surviving fish were retained in the tanks for other purposes.

The measured response for each fish used in the study was the elapsed time between placing the fish in the holding tank and death, removal, or the end of the study. This was referred to as survival time while the elapsed time between bringing the net on deck and placing the fish in the tank was defined as handling time. This latter measurement along with the length of the fish, depth trawled, and total catch were used as concomitant or explanatory variables for modeling the behaviour of survival time.

Methods commonly used to model survival time data identify potential probability models according to either the observed behaviour of the hazard function $h(t)$, where t indexes time, or the assumptions concerning $h(t)$ (Lawless 1982). The hazard function gives the instantaneous rate of death at time t given that a fish has survived until time t. This is formally expressed in terms of the probability density function, $f(t)$ and its distribution function, $F(t) = \int_0^t f(x)dx$, as,

$$h(t) = \frac{f(t)}{1 - F(t)}$$

$$= \frac{f(t)}{S(t)},$$

where $S(t)$ is referred to as the survivor function (i.e. probability of surviving until time t).

In most studies of survival time, including ours, not all of the animals die during the experiment and some may be removed before they die. In our case, live fish were sometimes removed from the holding tanks and sacrificed after 48 h to accomodate more experimental animals. In assessing mortality associated with capture, handling and release, we felt that 48 h after capture was a reasonable point to assess survival, as other studies indicated that mortality due to hyperactivity during capture usually occurred within 24 h of being caught (Black 1958; Beamish 1966; Peltonen 1969). Data from fish removed after 48 h are among those classes of observations referred to as 'right censored' (Aitkin and Clayton 1980; Lawless 1982). Such data contribute information to $S(t)$ only up to the time of removal or the end of the experiment, but allow no inferences concerning the nature of $f(t)$. The methods used here incorporate these observations in the estimation process assuming that the censoring is a random process (Aitkin and Clayton 1980; Lawless 1982). All fish which survived past the maximum of 50 d for the experiment duration were assigned the maximum survival time of 1200 h and treated as right censored observations.

In the analyses presented here, the relationships between the concomitant variables and survival time are modeled with respect to the hazard function. We used a class of models known as 'proportional hazards' models which relate the hazard function and explanatory variables in the form,

$$h(t|x) = h_0(t)g(x),$$

where $h_0(t)$ is some baseline hazard rate which is modified for each individual by the explanatory variables in x. Here we designate $g(x)$ to be $\exp[x\beta]$ where β is a vector of regression coefficients. This form ensures that the hazard rate remains positive and makes the model amenable to further examination using linear model theory. The probability distributions used for proportional hazards models include the exponential, Weibull, extreme value (or Gompertz), and Pareto distributions (Clayton 1983). All have monotonic hazard functions with respect to time. Initial choice of a model can be made by plotting the estimated cumulative hazard function $\hat{H}(t)$ against t and ln (t) with $\hat{H}(t)$ estimated as per Aitkin and Clayton (1980). An exponential distribution would be indicated when the plot of $\hat{H}(t)$ against t gave a straight line, while curvature implies a Weibull distribution. A Weibull distribution would also be indicated by a straight-line relationship between $\hat{H}(t)$ and ln (t), whereas curvature would indicate an extreme value distribution. Of course, heterogeneity in these plots may be a function of the explanatory variables and such plots would only be a rough first guide.

Estimates of the parameters in these analyses were obtained using GLIM (Generalized Linear Interactive Models Software, Payne 1986) and the methods given in Aitkin and Clayton (1980). The appropriate standard errors and confidence intervals were estimated according to the methods given in Aitkin and Clayton (1980) and Lawless (1982). Explanatory variables were fitted to the data and tested for inclusion in a linear model according to the amount of 'deviance' explained. The theory of Generalized Linear Models refers to deviance as the measure of discrepancy between the observed and fitted values (McCullagh and Nelder 1983) and the form of this measure is specific to the error distribution being used. The results of model fitting are portrayed here in Analyses of Deviance tables (for example see Table 3), where the significance of the amount of deviance accounted for by the inclusion of each covariate is tested with a χ^2 statistic. The column labelled 'scale' refers to the parameter in the mean to variance relationship, which for

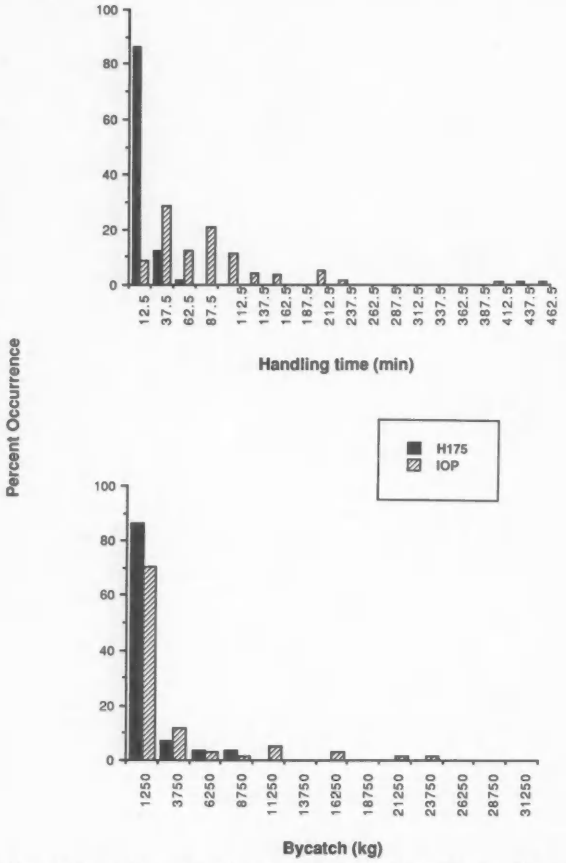

FIG. 2. Comparisons of total catch weight (excluding halibut) and handling time of catches from experimental fishing for Atlantic halibut with a Western IIA bottom trawl (Cruise H175, Sable Island Gully area), with data recorded by staff of the International Observer Program (IOP) stationed onboard commercial trawlers (April–August 1987).

the exponential and Weibull distributions is assumed to be 1.0. This statistic can be used as an additional diagnostic in assessing whether the choice of error distribution was appropriate.

Data Obtained from Observers Stationed on Commercial Fishery Trawlers

To obtain data on the condition of halibut from fishery observers onboard domestic trawlers, we designed a form to be completed whenever a set was made where halibut were caught. The observers were asked to qualitatively assess the condition of the halibut, and record information on set duration, fish length, handling time, and total catch weight. In this instance, condition was graded as follows: 1 — fish was lively, no scale loss, fins were intact, no other damage, 2 — minor damage (fish was alive, but with moderate scale loss, fin damage, or other injury), 3 — major damage (fish was alive, but with extensive scale loss, fin damage, or other injury 4 — fish was dead.

Results

Data Obtained from the Research Vessel

During the course of experimental fishing in the area of Sable Island Gully, halibut were collected on 32 otter trawl sets (422 fish, bottom depth range was 83–292 m) and on five strings of longline gear (48 fish, bottom depth range was 210–300 m). The distribution of total catch weight in the research vessel trawl is compared with data from the Observer Program (1981–87), as is handling time (Fig. 2). Typically, the smaller Western IIA trawl caught less than the commercial trawls and handling time on commercial vessels was considerably longer. Trawl durations during the experimental fishing were 120-min ($n = 13$), 110-min ($n = 1$), 100-min ($n = 1$), 49-min ($n = 1$), 35-min ($n = 1$), and 30-min ($n = 15$).

The length-frequency distributions of the longline and trawl catches during the experimental fishing indicated that the fish caught in the bottom trawl were considerably smaller than those taken by longline gear (t-test, $p < 0.001$). The types of injury observed for fish caught in bottom trawl and longline gear are summarized in Figs. 3 and 4, respectively. Data are presented as percentages of the total occurrence of a given injury type. To further facilitate interpretation, the data were stratified by three length class intervals and body areas of the fish. The most common injury types in trawl-caught fish were the "slight damage" (Code 1) and "scales missing" (Code 2) categories, most commonly found on the pigmented side of the fish, on the posterior two-thirds of the fishes' bodies. Fish in the largest size category had relatively few wounds of any description. Although the number of descriptions of injuries available for the longline-caught fish was comparatively small (28 versus 187 for Western IIA), some differences in the patterns of wounds were apparent. A comparatively high (16 of 28) proportion of fish had open wounds in the head region (unpigmented side), which was associated with the penetration of the hook through the region of the operculum. Scale loss was never found on fish caught with longlines.

Of fish less than the proposed size limit caught during the research vessel experiment, only 35% taken in bottom trawl sets of 120-min duration survived more than 48 h, whereas 77% of longline-caught fish survived. The number (with percents shown in parentheses) of all observations (fish of all sizes, all set durations) which were fishing mortalities, tank mortalities, released, sacrificed, kept or had data lost (due to events such as tag loss) are shown below, by gear type.

	Western IIA	Longline
Fishing mortality	20 (4.7)	1 (2.1)
Tank mortality	304 (72.0)	7 (14.6)
Released	23 (5.5)	4 (8.3)
Sacrificed	44 (10.4)	12 (25.0)
Kept	7 (1.7)	23 (47.9)
Data lost	24 (5.7)	1 (2.1)

As indicated in the methods, fish larger than the proposed minimum size were sometimes released or sacrificed, thus avoiding unduly crowded conditions in the holding tanks onboard the research vessel.

To examine factors which influenced survival while simulating commercial fishing practices, we divided trawl durations into two groups: 100–120 min (long tows) and 30–49 min (short tows). Of the fish caught, 20 (14 of 271 from 15

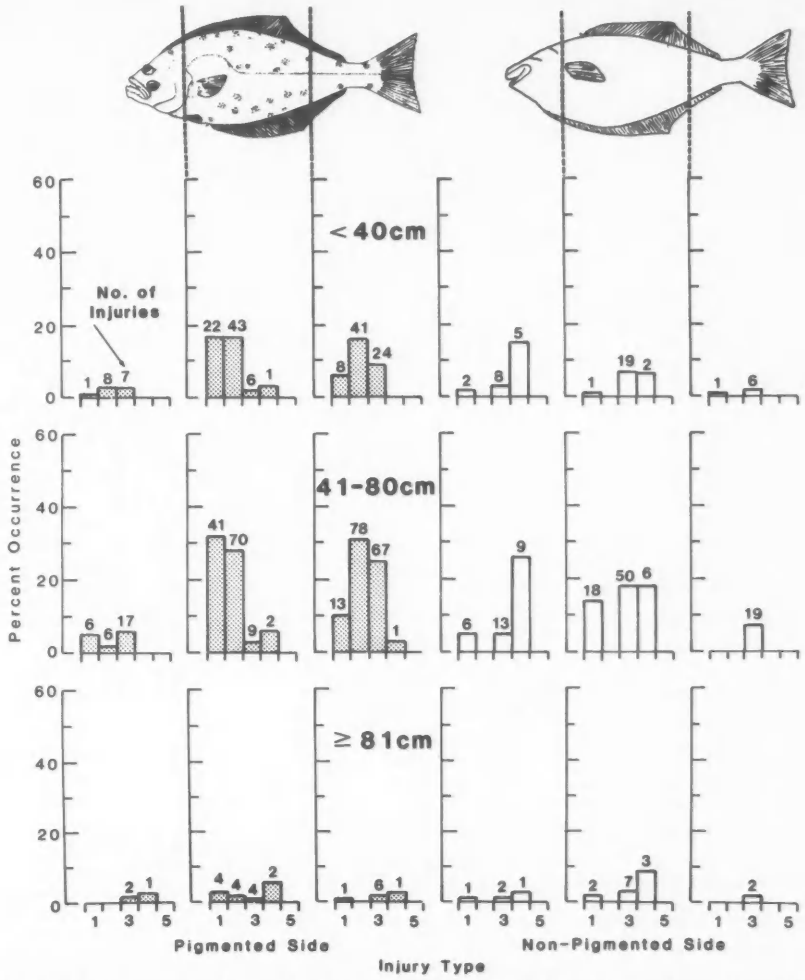

FIG. 3. Percent occurrence of injury types in trawl-caught Atlantic halibut. Injury codes are: 1 — slight damage; 2 — scale loss; 3 — redness, bruising; 4 — open wounds; 5 — damaged jaws. Data are stratified by fish length class and body region. Observations of any injury type total 100% when summed across length class and body region. Sable Island Gully, June/July 1987.

long tows and 6 of 151 from 17 short tows) were dead when the net was retrieved. After accounting for such mortalities fish released for other purposes, and missing data, there remained 226 fish from the long tows and 107 from the short tows (with the exclusions, short tows were all of 30-min duration). The longline gear provided 48 fish, of which 31 fish were used in the survival experiment. Only one of the longline fish was reported dead on capture.

Data used in the proportional hazards modeling were from fish of 29–57 and 29–96 cm in length for the short and long tows, respectively. Longline fish were between 62–111 cm. Mean survival times for those animals which died during the experiment (uncensored) and for the combination of right-censored and uncensored observations are given in Table 1 for both tow durations from the trawler catches and from the longline catches. The fish from the long duration sets were grouped into several size categories to better examine the effect of fish size on survival. The grouping of 29–81 cm for trawl-caught fish was included to correspond with the proposed minimum size regulation. For all but the 29–57 cm fish from the long tows, the addition of the censored data increased the mean survival times compared with the corresponding values derived from the uncensored cases. Because the censored times only provide an approximation of minimum survival times, these latter means are underestimates of what the true means would be if all of the animals were allowed to die naturally. The length of tow has an effect on the survival time, and there appears to be an effect due to the size of the fish in the long tows. There is also a difference due to gear (Table 1).

The plot of $\hat{H}(t)$ versus ln (t) (Fig. 5) for the trawl-caught fish indicated that the Weibull distribution was appropriate for those data, as there appeared to be a straight-line relationship. However, since differences in means were found with respect to tow duration, the assumption regarding distribution type was examined for each fish length and tow duration group identified above (Table 2). The Weibull

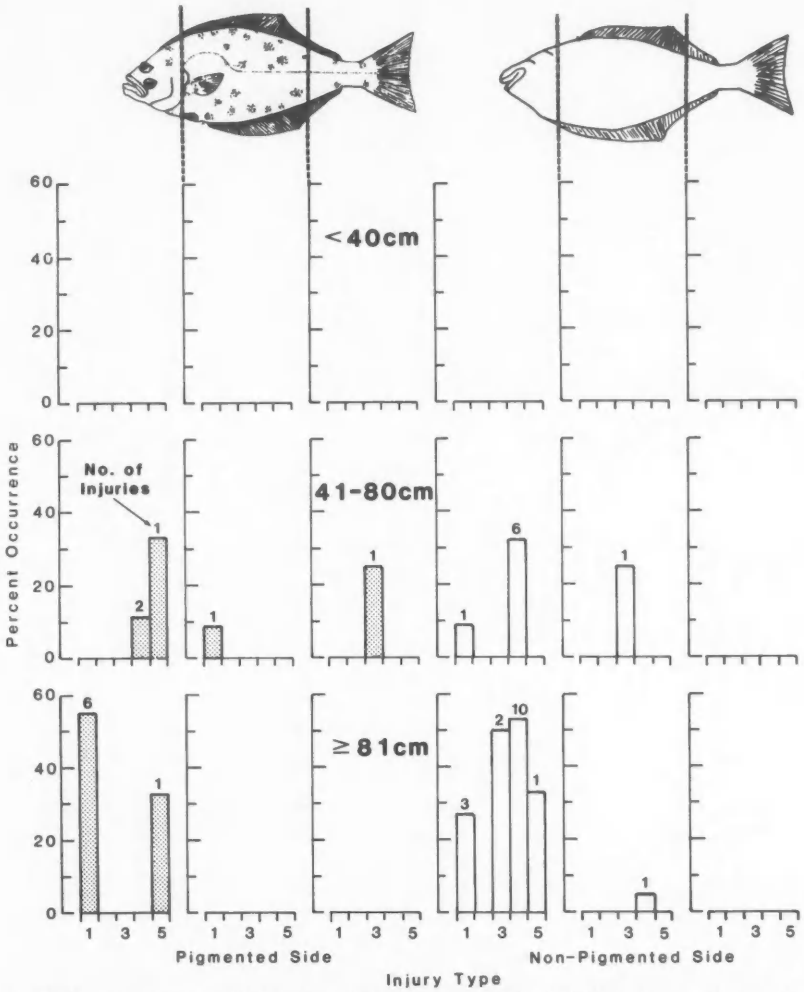

FIG. 4. Percent occurrence of injury types in longline-caught Atlantic halibut. Injury codes are: 1 — slight damage; 2 — scale loss; 3 — redness, bruising; 4 — open wounds; 5 — damaged jaws. Data are stratified by fish length class and body region. Observations of any injury type total 100% when summed across length class and body region. Sable Island Gully, June/July 1987.

TABLE 1. Mean survival times (hours) from the Atlantic halibut experiment. Sable Island Gully, June/July 1987. "All observations" refers to the combination of right censored and uncensored observations.

Case (sample size)	Length interval (cm)	Mean survival time	
		Uncensored	All observations
Short tow (107)	29–57	110.75	151.47
Long two (226)	29–96	53.01	63.80
	29–57	53.35	53.12
	29–81	52.78	63.27
	58–96	56.05	114.99
Longliner (31)	62–111	219.70	942.00
	62–81	144.80	788.00

distribution given below corresponds to an exponential distribution when the parameter $\alpha = 1$:

$$f(t) = \alpha t^{\alpha-1}\exp[x\beta - t^{\alpha}\exp(x\beta)],\ (t \geq 0, \alpha > 0).$$

The hypothesis that $\alpha = 1$ was tested for each of the groups and the Weibull assumption appears to be appropriate for all of the cases (Table 2). However the individual estimates of α vary considerably from case to case. The hazard function for the Weibull distribution is,

$$h(t|x) = \alpha t^{\alpha-1}\exp(x\beta),$$

and with $\alpha < 1.0$, a decreasing hazard rate is implied for all the cases. The duration of the tow and the type of gear appeared to affect the hazard rate and therefore the data from each of the tow durations and gear types was analyzed separately. The distributional assumption was reexamined again for the residuals from each case once the final models were determined.

Linear models were fitted to the survival data using the covariates length, handling time (in minutes), depth trawled, and total fish catch for each of the trawl-caught groups. Length was the only covariate measured for the longline-caught fish. The resulting analyses of deviance are given in Tables 3 and 4.

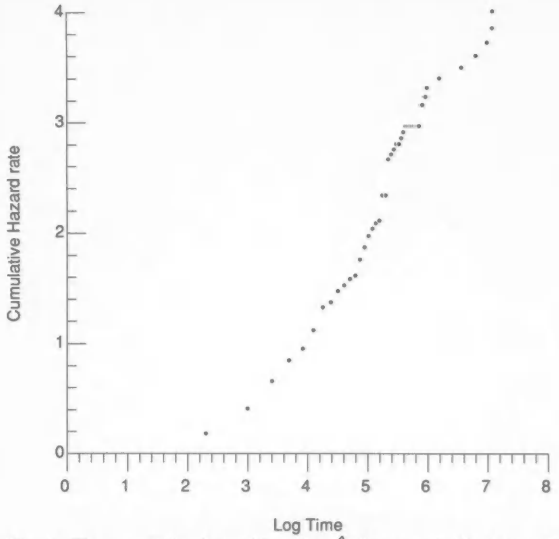

FIG. 5. The cumulative hazard function $\hat{H}(t)$ versus ln (t), for trawl-caught Atlantic halibut. Sable Island Gully, June/July 1987.

TABLE 2. Results of fitting exponential distribution versus Weibull distribution for the Atlantic halibut survival data. The p-level is for a χ^2-test.

Case	Deviance			
	Exponential	Weibull	$\hat{\alpha}$	p-level
Short tow (29–57 cm)	195.31	176.90	0.7964	0.0009
Long tow (29–57 cm)	422.79	351.05	0.6672	0.0000
(29–81 cm)	533.59	438.57	0.6402	0.0000
(57–96 cm)	70.85	63.63	0.6884	0.0413
Longliner (62–11 cm)	53.05	45.57	0.4309	0.0291

For short tows and fish of lengths 29–57 cm, models which included either ln catch, catch or length were significant ($p < 0.05$). The final model for the survival of fish from the short tows consists of ln(catch) and length while the model including the interaction between the two (denoted as "len.ln catch" in Table 3a) was not significant.

All covariates examined individually resulted in significant reduction in deviance for fish of the same size range from long tows. However, conditional on the inclusion of handling time, only the effect of length was significant, and even then, only marginally so (Table 3b). Therefore, the final model included handling time only. The assumptions regarding the choice of error distribution were assessed by testing whether $\alpha = 1$ for the final models. The results of the tests indicated that fish from the tows of short duration exhibited an exponential hazard rate (p-level = 0.1677) after the covariates had been included, while the hazard rate for those fish of the same size from long set durations were well described by a Weibull model (p-level < 0.00001). Residuals from the two models were examined by plotting the quantiles from their respective residuals against the quantiles from the standard exponential distribution (Figs. 6 and 7). Neither show any serious deviations from the 1:1 line, indicating that the models fit the data quite well. However, the scale parameter estimate of 1.87 and 1.37 for the final models from the long and short tows, respectively, indicate some degree of over-dispersion in the residuals relative to the error model assumptions.

There was some difficulty in modeling the data set as a whole for long tows. Fish larger than 57 cm were often associated with

TABLE 3. Analysis of deviance for (a) short tows (30 min) and (b) long tows (100–120 min) for fish 29–57 cm in length. The p-level is for a χ^2-test. Scale refers to the parameter in the mean to variance relationship (see text). Variables labelled as follows: catch = total catch all species; ln catch = logarithm of total catch, all species; length = individual halibut lengths (centimetres); depth = maximum depth trawled; hand = handling time (minutes).

Model	Reduction in deviance	DF	p-level	Scale
(a) Short Tows				
1				
+ Ln catch	28.10	1	0.0000	1.84
+ Catch	15.86	1	0.0023	1.59
+ Length	13.37	1	0.0055	1.71
+ Depth	1.77	1	0.3278	1.73
+ Hand	1.40	1	0.3847	1.84
				1.85
+ Ln catch				
+ Length	24.48	1	0.0000	1.37
+ Len.ln catch	1.09	1	0.3717	1.38
(b) Long tows				
1				2.27
+ Hand	77.00	1	0.0000	1.87
+ Depth	4.77	1	0.1087	1.85
+ Length	7.55	1	0.0500	1.84
+ Catch	0.04	1	0.8776	1.88
+ Ln catch	0.36	1	0.6603	1.88
+ Depth	47.65	1	0.0000	2.03
+ Length	20.76	1	0.0020	2.17
+ Catch	15.22	1	0.0086	2.20
+ Ln catch	13.04	1	0.0153	2.21

TABLE 4. Analysis of deviance for (a) fish 57–96 cm and (b) longliner-caught fish. The p-level is for a χ^2-test. Scale refers to the parameter in the mean to variance relationship (see text). Variables labelled as follows: catch = total catch, all species; length = individual halibut lengths (centimetres); depth = maximum depth trawled; hand = handling time (minutes).

(a) Long tows (57–96 cm)				
Model	Reduction in deviance	DF	p-level	Scale
1				1.86
+ Catch	13.03	1	0.0039	1.56
+ Length	9.76	1	0.0150	1.65
+ Hand	5.64	1	0.0736	1.76
+ Ln catch	4.55	1	0.1109	1.79
+ Depth	1.61	1	0.3526	1.87
+ Catch				
+ Length	4.90	1	0.0689	1.47
(b) Longliner caught fish				
1				1.77
+ Length	2.45	1	0.2361	1.74

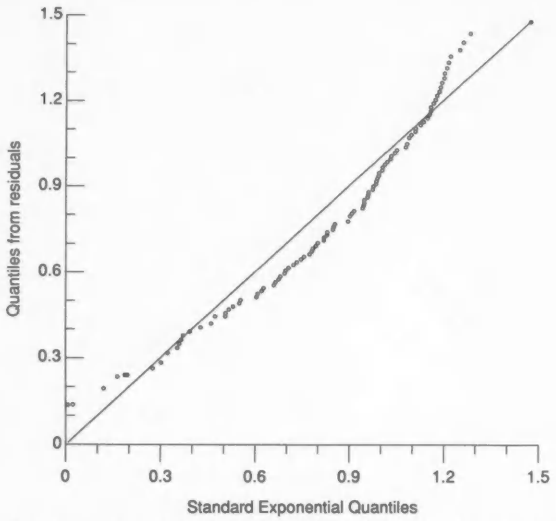

FIG. 6. Residual quantile–quantile plot for the model "$b_0 + b_1$(len) + b_2(ln catch)." Trawl-caught Atlantic halibut, short tows. Sable Island Gully, June/July 1987.

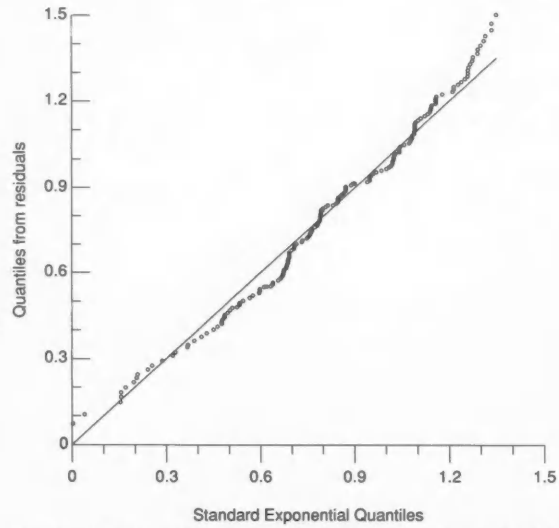

FIG. 7. Residual quantile–quantile plot for the model "$b_0 + b_1$(hand)." Trawl-caught Atlantic halibut, long tows, fish ≤57 cm. Sable Island Gully, June/July 1987.

longer handling times, larger catches, and deeper depths than the smaller fish. Such associations resulted in significant interactions terms and confounding effects. Therefore, the analysis was confined to only two groups of fish from the long tows: fish ≤57 cm and those >57 cm. The analyses of deviance for the latter group and for the longline-caught fish are given in Table 4. Total catch appears to be the only significant covariate for the large fish in the long tows while length was not significantly related to survival for the longline fish. The test for exponential versus Weibull distribution indicated that the larger trawl-caught fish exhibited an exponential hazard rate (p-level = 0.2685) while the survival

TABLE 5. Parameter estimates and expected survival times (with 95% confidence intervals) for exponential regression models. Confidence intervals are large-sample estimates (Lawless 1982; p; 292–294). The parameters being estimated are for the relationship $h(t|x) = \exp[x\beta]$. (Total catch is expressed as the first three quartiles of the observed catch weights in the experiment).

(a) Short tows (29–57 cm). Model = 1 + ln catch + length, Scale = 1.37

Parameter	Estimate	SE
β_0	0.3803	0.7831
β_1	−0.3924	0.0663
β_2	−0.0841	0.0162

Expected survival times (h)

Length (cm)	Total catch (kg) 29.0	62.0	295.0
30	31.95 (20.47, 49.80)	43.04 (28.57, 64.85)	79.38 (52.70, 119.56)
40	74.07 (58.19, 94.28)	99.80 (81.66, 121.97)	184.06 (142.87, 237.14)
50	171.75 (134.93, (218.61)	231.41 (164.83, 324.88)	426.78 (284.89, 639.34)

(b) Long tows (>57 cm). Model = 1 + catch, Scale = 1.56

Parameter	Estimate	SE
β_0	−6.1730	0.3396
β_1	0.0004	0.00009

Total catch (kg)	Expected survival time (h)	95% Confidence intervals Lower	Upper
332	420.31	225.58	783.14
1163	301.21	178.05	509.54
3640	111.83	68.45	182.71

times of longline fish are better described by a Weibull distribution (Table 2).

Estimates of model parameters and predicted survival times for all of the above cases are given in Tables 5 and 6. The confidence intervals are large sample estimates obtained from methods given in Lawless (1982, p. 292–294, 310–313). The total catch weights associated with estimated survival times given in Table 5 correspond to the first, second, and third quartiles of the actual catch weights observed for each case. In Table 5a, total catch is negatively related to the hazard rate while the opposite is true in 5b. This apparent contradiction becomes less so when the much larger catches observed in the long tows are considered.

Data Obtained from Observers Stationed on Commercial Fishery Trawlers

Over the period April 6 to August 22, 1987, staff of the International Observer Program collected data on 124 halibut from 76 sets. The fish were 41–178 cm in length, with a mean of 92.3 cm. Most (75.8%, 94 of 124) of the fish were assigned to the highest condition grade, with 16.5% (19 of 124) considered dead when examined. A further 11 fish (8.9%) were judged to have suffered minor damage. Among the fish which were dead when examined, 5 of 19 were associated with long (>400 min) sort duration and large catch weights (>15 000 kg). Apart from those mortalities, no trends were apparent in the relationship

TABLE 6. Parameter estimates and expected survival times for Weibull regression models. Confidence intervals are large-sample estimates (Lawless 1982; p 310–313). The parameters estimated for the Weibull regression model are for the relationship $h(t|x) = \alpha t^{\alpha-1}\exp[x\beta]$, where x is the matrix of the covariates.

(a) Long tows (29–57 cm). Model = 1 + hand, Scale = 1.67

Parameter	Estimate	SE
α	0.7461	0.03979
β_0	−3.7540	0.27466
β_1	−0.0657	0.00985

Handling time (min)	Expected survival time (h)	95% Confidence intervals	
		Lower	Upper
1	167.71	99.37	283.06
10	75.92	44.98	128.14
20	31.47	18.65	53.12
30	13.05	7.73	22.02

(b) Longlines. Model = 1, Scale = 1.57

Parameter	Estimate	SE
α	0.4309	0.07655
β_0	−4.3720	0.64786

Expected survival time (h)	95% Confidence intervals	
	Lower	Upper
69 961.5	14 444.97	338 845.53

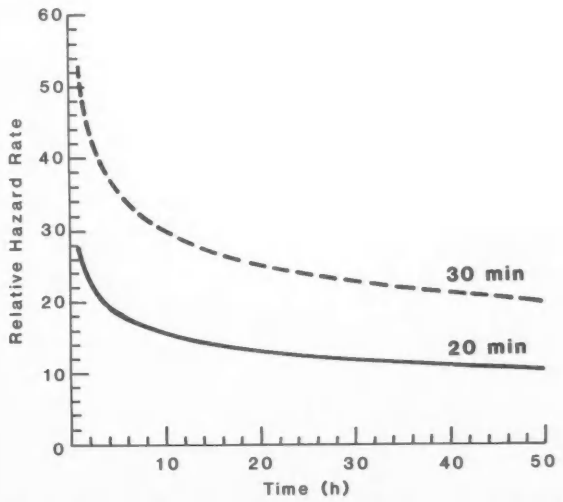

FIG. 8. The relative hazard rate for Atlantic halibut caught in tows of long duration compared with short tows. The fish length was 50 cm, the total catch weight was 300 kg, and the relative hazard rate is shown for handling times of 20 and 30 min. Sable Island Gully, June/July 1987.

of survival code to handling time, total catch size, fish length, or trawl duration.

Discussion

The probability models for survival time developed here allows for predictions of the proportion of fish that would survive past a certain point in time. For example, the predicted percentage of fish which would survive past 48 h is given below. The choice of the covariates reflects those which proved to be significant in the analyses of deviance (Tables 3 and 4).

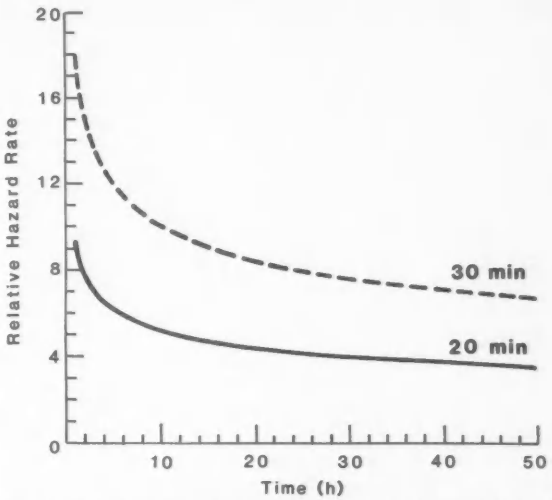

FIG. 9. The relative hazard rate for large (>57 cm) Atlantic halibut caught in tows of long duration compared with small (≤57 cm) fish. The total catch weight was 3000 kg, and the relative hazard rate is shown for handling times of 20 and 30 min. Sable Island Gully, June/July 1987.

	Covariates	Percent surviving
Short tows (≤57 cm)	Length = 30 cm	
	Total catch = 29 kg	22.3
	Total catch = 62 kg	32.8
	Total catch = 295 kg	54.7
	Length = 40 cm	
	Total catch = 29 kg	52.3
	Total catch = 62 kg	61.8
	Total catch = 295 kg	77.0
	Length = 50 cm	
	Total catch = 29 kg	75.6
	Total catch = 62 kg	81.3
	Total catch = 295 kg	89.4
Long tows (≤57 cm)		
	Handling time = 1 min	67.5
	Handling time = 10 min	49.2
	Handling time = 20 min	25.5
	Handling time = 30 min	7.2
Long tows (>57 cm)		
	Catch weight = 330 kg	89.2
	Catch weight = 1163 kg	85.3
	Catch weight = 3640 kg	65.1
Longline (all sizes)		99.0

The results above give somewhat contradictory indications with regard to the effect of total catch weight on survival. In tows of short duration, survival rate is positively correlated with catch weight, whereas in longer tows, the relationship is negative. Although speculative, we surmise that a certain comparatively small level of bycatch may positively affect survival as other fish might provide a cushioning effect, or reduce abrasion against net twines. However, with greater total catch weights, crushing and suffocation within the codend might occur more frequently, thus reducing survival rates.

The survival estimates are contingent upon the assumptions that the mortality observed in the holding tanks reflects that which fish would have encountered had they been released, and that no significant mortality attributable to capture and handling occurred after 48 h. The high mortality observed in trawl-caught halibut together with the continued mortality after 48 h bring the validity of those assumptions into question. In support of our premise, we note that the survival of longline-caught fish, held in identical conditions to the trawl-caught fish, was relatively high. However, this inference is confounded to some extent by the observations that longline-caught fish were larger on average, and larger fish seemed to survive longer (Table 1). Concerning the continued mortality of trawl-caught fish 48 h after capture, we conclude that much of this was related to secondary infection, namely finrot (genus *Flexibacter*). Without excluding the importance of secondary infections in nature, we feel that the unnatural crowding in the holding tanks probably contributed to the spread of the infection. Undoubtedly, other secondary causes of death such as osmotic failure related to scale loss or internal damage were also involved. A potential shortcoming of our approach is that the models used here implicitly require that causes of mortality do not change over time. Therefore, we have less confidence in our predictions beyond the 48-h period. However, in support of the long predicted survival times indicated by our model for longline-caught halibut (Table 6), many such fish are alive at the time of writing, 10 mo after their capture.

The examination of external injuries in trawl-caught and longline-caught fish (Figs. 3 and 4) supports the view that trawl-caught fish sustained greater damage than did longline-caught fish. For example, longline-caught fish did not suffer any visible scale loss, whereas such an injury was quite common in trawl-caught fish. Scale loss and damage to the integument is thought to stress the osmoregulatory ability of fish (Parry 1966) and may lead to an increased rate of secondary infection. Hence, differences in type and extent of external injury may at least partially account for the higher survival of longline-caught fish.

The relative hazard rates for fish caught in short duration tows versus long duration tows were compared for two handling times in Fig. 8. The relative hazard rates were calculated as a ratio of the expected hazard rates from the model given for each tow duration (Tables 5a and 6a) for fish of a given size (50 cm), handling time (20 or 30 min) and total catch weight (300 kg). A fish released after 20 min handling time is about 28 times as likely to die after 1 h if caught in a set of long duration than would be the case if it was taken in a set of short duration. This relative hazard would be increased to 54 times for the same conditions after 30 min of handling. Therefore, the effect of the longer tow duration is to increase the rate of mortality with this rate being further increased by longer handling times. After a period of time, the effect of handling time and/or tow duration is reduced and the hazard rate reaches an asymptote. Given a 3000 kg catch weight, a halibut $\leq$57 cm is 18 times more likely to succumb after 1 h than a fish >57 cm (Fig. 9). Once again, decreased handling time would improve the likelihood of survival. A further outcome of our findings is that there will probably be a higher proportion of fish returned to the water which die in the more southerly regions (Scotian Shelf, Gulf of St. Lawrence) compared with the situation off Newfoundland and Labrador, as the lengths of halibut captured in the more northerly fisheries are known to be greater (Neilson et al. 1987).

Our results are consistent with Hoag (1975) for Pacific halibut, who found that the condition of fish was positively correlated with length of fish and negatively correlated with time on deck and weight of total catch. Kelle (1976) also found a relationship between total catch weight and survival of small flatfish (sole (*Solea solea*), dab (*Limanda limanda*), and plaice (*Pleuronectes platessa*)) in a German shrimp fishery. In our case, there may be other factors not measured which had a significant influence on halibut survival in the holding tanks. For example, internal injuries might have been responsible for the unaccounted variability, or variations in the speed of the trawl through the water as a result of tidal action. A further source of variability in survival time is the type of bycatch. Bell (1956) demonstrated that the survival of trawl-caught Pacific halibut was negatively correlated with the occurrence of spiny dogfish (*Squalus acanthias*) as bycatch and Kelle (1976) showed that the occurrence of *Pleurobrachia* sp. and *Cyanea* sp. positively influenced the survival rate of small flatfish when such gelatinous zooplankton occurred in the bycatch in large quantities. Perhaps most importantly, while tow duration is included as a factor, there is no way of assessing at what point fish were actually captured in the trawl. Tow durations therefore represent the maximum time which fish were enclosed by the net, when in fact fish could have spent considerably less time within the trawl.

Our results demonstrate the danger in employing visual assessment of condition as an indicator of future survival should the fish be released. Using criteria similar to those employed by Hoag (1975), observers onboard the fishing vessels indicated that about 75% of trawl-caught halibut were in excellent condition. During the course of the experimental fishing, we often caught halibut which appeared to be in excellent condition, yet such fish often succumbed later while in the holding tanks. A further implication of this work is that investigators planning studies of halibut involving handling of the fish, such as tagging, should be aware of the deleterious effects of extended handling on survival and plan their work accordingly.

Acknowledgments

While many contributed to this work, we especially wish to acknowledge the contribution of the scientific staff onboard our cruise: M.-I. Buzeta, K. Howes, and P. Perley. The assistance of G. Dedrick with the longlining operations was essential to the success of this study. We also wish to thank Prof. J. Lawless, University of Waterloo, for helpful discussions regarding proportional hazard modeling. Prof. D. Hamilton, Dalhousie University, Dr. W. Stobo, Department of Fisheries and Oceans, and Dr. S. H. Hoag, International Pacific Halibut Commission provided critical reviews of an earlier version of the manuscript. Mr. M. Showell, Department of Fisheries and Oceans, arranged the collection of data from the commercial trawlers. Finally, we thank Captain N. Barnes and crew of the *Lady Hammond* for their enthusiasm and assistance in undertaking a rather unusual study. We also thank W. McMullon with assistance in drafting some of the figures, and Ms. Darlene Warren for proof-reading the manuscript.

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Potential for Predicting Plankton Populations (and Fish Recruitment) from Environmental Data

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Evans, G. T., and P. Pepin. 1989. Potential for predicting plankton populations and fish recruitment from environmental data. Can. J. Fish. Aquat. Sci. 46: 898–903.

A model of annual plankton cycles, which responds to seasonal changes in light and mixed layer depth, was driven by a 26-yr series of observed mixed layer depths. Within the model, year-to-year changes in herbivore concentration are completely determined by year-to-year changes in mixed layer depth; but a correlational study of these two variables does not reveal the dependence, especially for spring herbivore concentrations. Fish recruitment, to the extent that it depends on the timely availability of planktonic food, may be difficult to relate to environmental observations. There are, however, some weak but long-lasting correlations which adult fish may be able to use as a cue for allocating reproductive effort.

Un modèle représentant les cycles annuels du plancton, qui répond à des modifications saisonnières de la lumière et de la profondeur de la couche mélangée, a été entraîner par observations de la profondeur de la couche mélangée échelonner sur une période de 26 années consécutives. Dans ce modèle, les changements d'une année à l'autre de la concentration d'herbivores sont déterminés par les modifications d'une année à l'autre de la couche mélangée; cependant, une étude corrélationnelle de ces deux variables n'a pas mis en évidence la dépendance, notamment dans le cas des concentrations d'herbivores mesurées au printemps. Il est peut être difficile d'établir une relation entre le recrutement des poissons, dans la mesure où il dépend de la disponibilité opportune de nourriture planctonique, et des observations de la condition de l'environnement. Cependant, il existe de faibles corrélations de longue durée que les poissons adultes peuvent être en mesure d'utiliser pour déterminer l'allocation des efforts de reproduction.

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Simple models of plankton population dynamics can exhibit many features that are observed in real populations. Periodic annual variation in light and mixed layer depth can lead to spring phytoplankton blooms (Evans and Parslow (1985) and seasonal succession of phytoplankton species (Evans 1988). Within the models, we know that annual variation in the physical variables causes annual variation in the populations: the latter would not vary if the former did not. Short of solving the equations, we cannot summarize exactly how physical variation causes population variation: the population dynamic effects take time to work themselves out, so that the causal links are not immediate or obvious.

Mixed layer depth varies between as well as within years, and this causes plankton populations to vary between years. Although model populations can vary between years even if the physics repeats exactly from year to year (Evans 1988), it is reasonable to regard the interannual part of the variation in populations as a deterministic function of the interannual part of the variation in the physics. It is even more true here that, although there is a precise deterministic causal link between the physics and the populations, this link is neither immediate nor obvious.

In nature, interannual variations in physics must influence population dynamics, but the correct model for the influence is unknown. People often seek to demonstrate an influence using product–moment or rank–order correlations, which assume a linear or monotonic model. This paper explores how well such an approach can be expected to work. We run a population dynamics model whose response to physical variation is reasonably complicated, but in which we know how all the causes vary, there is no random component, and there is no measurement error. We then calculate correlations between environmental input and zooplankton output. The results should indicate an upper bound on the predictability of real plankton populations, which have more complicated dynamics, more unobserved causal variables, and more noise.

One reason for studying predictability is that predictions are contemplated on an even grander scale. The size of year-classes recruiting to a fish stock can vary greatly between years, even allowing for differences in spawning stock size. It is commonly believed that much of the extra variation is caused by environmental influences on survival of young fish: perhaps because the environment affects plankton concentrations, and planktonic food, over the whole larval period or some important subset of it, affects fish larval survival (Johansen 1927; Marr 1960; Dickson et al. 1974). Fluctuations in zooplankton abundance and the timing of spring bloom zooplankton might therefore appear, amplified, in year-class strengths. Arguments like this have persuaded people to seek correlations with environmental variables like freshwater runoff, temperature, or upwelling indices (Shepherd et al. 1984). However, others have failed to detect a link between zooplankton and larval survival (Leak and Houde 1987; Rice et al. 1987; Taggart and Leggett 1987). This

paper inquires whether a link between environment and zooplankton can be detected.

Model

We used the model of Evans (1988), which simulates plankton population dynamics in a horizontally and vertically homogeneous upper mixed layer. The depth, M, of the mixed layer changes at a prescribed rate $\zeta(t)$. A representative time series for ζ was obtained from hydrographic casts made, roughly bimonthly, at Station 27, near St. John's, Newfoundland from 1959 to 1984 (S. A. Akenhead, Department of Fisheries and Oceans, St. John's, Newfoundland, unpubl. data). The details are not crucial, because the mixed layer of the model, with infinite mixing within the upper layer and finite exchange across a sharp boundary, is a caricature of the real mixed layer with finite and variable mixing throughout. The cycle in any year was described by six numbers, which vary between years: the depths of the summer and winter mixed layers, and the times of the start and end of spring shallowing and autumn deepening (Fig. 1).

The model ecosystem comprises dissolved nutrients, N, two groups of phytoplankton species, P and Q, each similar enough to be represented by a common set of parameters, and herbivorous zooplankton, H. As the mixed layer deepens, it dilutes the quantities in the upper layer, and introduces nutrients; as it shallows it concentrates herbivores (which can swim up) but not nutrients or phytoplankton. Nutrients and phytoplankton are also mixed across the bottom of the mixed layer, and phytoplankton sink. For each phytoplankton group, the photosynthetic rate is a function $\phi(t, M, P, Q)$ of time of year, mixed layer depth, and phytoplankton concentrations (because of shading). Growth is reduced by nutrient limitation, according to a Michaelis–Menten hyperbola, and by a constant soluble metabolic loss term. Grazing of phytoplankton by herbivores is modelled by a Michaelis–Menten hyperbola, above a threshold concentration. Losses to carnivores are simulated by constant mortality of the herbivores. The model equations are:

$$\frac{dM}{dt} = \zeta(t)$$

$$\frac{dN}{dt} = \frac{m+\zeta^+(t)}{M}(N_0 - N) - \left[\frac{\phi(t, M, P, Q)N}{j+N} - r\right]P - \left[\frac{\phi'(t, M, P, Q)N}{j'+N} - r'\right]Q$$

$$\frac{dP}{dt} = \left[\frac{\phi(t, M, P, Q)N}{j+N} - r\right]P - \frac{pP}{A}\frac{c(A-P_0)H}{A+k-P_0} - \frac{m+s+\zeta^+(t)}{M}P$$

$$\frac{dQ}{dt} = \left[\frac{\phi'(t, M, P, Q)N}{j'+N} - r'\right]Q - \frac{qQ}{A}\frac{c(A-P_0)H}{A+k-P_0} - \frac{m+s'+\zeta^+(t)}{M}Q$$

$$\frac{dH}{dt} = \frac{fc(A-P_0)H}{A+k-P_0} - gH - \frac{\zeta(t)}{M}H,$$

where the meanings of the parameters are given in Table 1, $\zeta^+(t) = \max(\zeta(t),0)$, and $A = pP + qQ$ is the total phytoplankton as perceived by herbivores. The year is 360 days long, starting on the shortest day. Evans and Parslow (1985) and Evans (1988) described the model in more detail.

To eliminate starting transients, we ran the model for 2 yr with the average annual depth cycle; these first 2 yr do not enter subsequent analyses. Because the model is known to be sensitive to some parameter changes, we repeated the procedure with seven different parameter sets, having different values for deep nutrient concentration N_0 and vertical mixing rate m as follows:

N_0	9	10	8	11	12	9	9
m	1.8	2.6	1.2	1.8	2.4	0.3	0.35

Correlation Analysis of the Output

The model has a 26-yr series of mixed layer depths as input, and a 26-yr series of herbivore concentrations as output. To

TABLE 1. Model parameters. mM means millimoles of nitrogen. Parameters with greek symbols are not referred to in the equations; they enter the calculation of photosynthetic rates (Evans and Parslow 1985).

Parameter	Symbol	Units	Value	
Deep nutrients	N_0	m$M\ m^{-3}$	see text	
Grazing threshold	P_0	m$M\ m^{-3}$	0.1	
Grazing half saturation	k	m$M\ m^{-3}$	1.0	
Maximum grazing rate	c	d^{-1}	1.0	
Grazing efficiency	f	—	0.5	
Loss to carnivores	g	d^{-1}	0.07	
Vertical mixing rate	m	$m\ d^{-1}$	see text	
Light attenuation by water	γ	m^{-1}	0.10	
Latitude	λ	degrees	47	
Cloud cover	ν	—	0.9	
			P	Q
Uptake half saturation	j	m$M\ m^{-3}$	0.5	1.2
Plant metabolic loss	r	d^{-1}	0.04	0.07
Sinking rate	g	$m\ d^{-1}$	1.0	0.0
Palatability to herbivores	p, q	—	1.0	0.4
Maximum photosynthetic rate	μ	d^{-1}	2.3	3.2
Low light photosynthetic slope	α	$(ly)^{-1}$	0.04	0.0205
Light attenuation by phytoplankton	β	$(\text{m}M\ m^{-2})^{-1}$	0.0	0.1

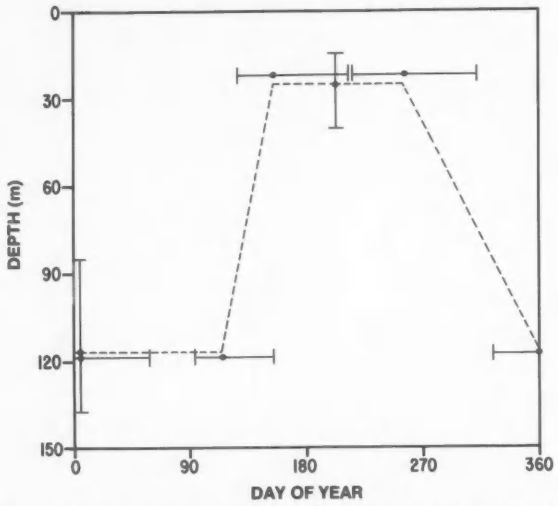

FIG. 1. Average annual cycle of mixed layer depth ζ at Station 27, and the variation among years in the six numbers that describe it.

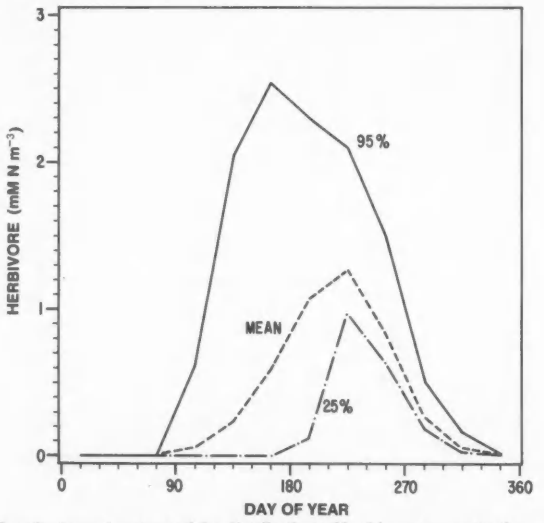

FIG. 2. Annual pattern of the distribution of herbivore concentrations, over 26 yr and seven parameter sets, represented by the mean and 95th and 25th percentiles.

mimic the sort of analysis that is done, or the sort of information that is likely to be collected by research cruises, we reduced a year's input and output to a single number each. We chose to relate the herbivores, averaged over a 30-d interval within the year, to the mixed layer depth averaged over some other 30-d interval between 0 and 360 d earlier. We calculated Kendall's nonparametric rank correlation coefficient τ, where $(1 + \tau)/2$ is the probability that a change in one variable will be accompanied by a change in the same direction in the other. The assumed relation is monotonic — a weaker assumption than linearity. Because there is nothing special about either interval, we calculated τ as a function of time of year (for herbivores) and lag.

Although the multitude of tests, and the correlation among months and among parameter sets, vitiate any calculation of

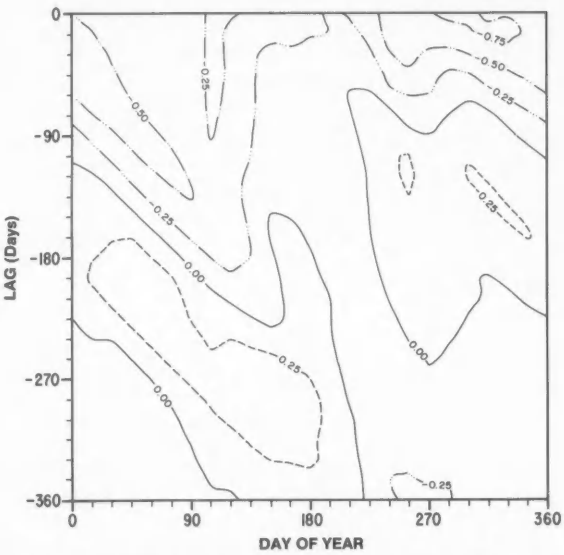

FIG. 3. Contours of Kendall's τ for monthly average herbivores in different months (horizontal axis) versus monthly average mixed layer depth 0 to 360 d earlier (vertical axis). Points representing mixed layer depth at a particular time of year lie along a 45° diagonal line sloping down to the right. The convention for all contour diagrams is that broken lines represent positive correlations and broken and dotted lines represent negative correlations.

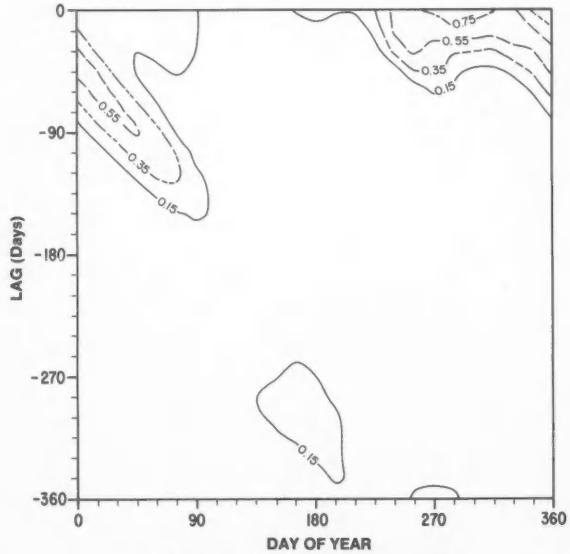

FIG. 4. Contours of r^2 for the same variables.

statistical significance, we note that in a single test of 26-yr series, $|\tau| > 0.28$ would be significant at the 0.05 level.

Results

The predictability was not greatly influenced by the particular parameter set, and therefore we present τ's averaged over

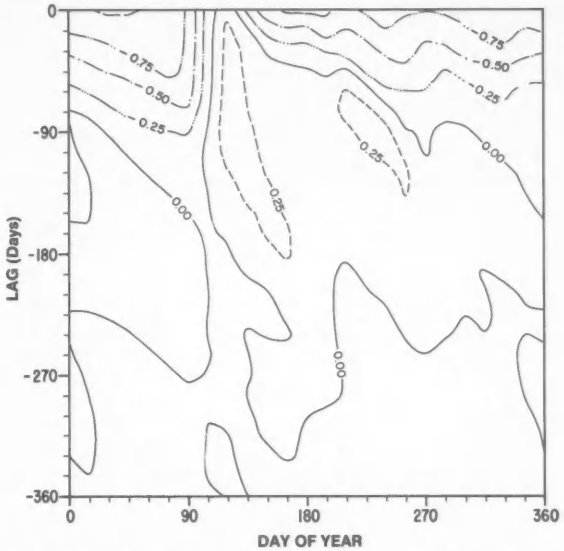

FIG. 5. Contours of τ for herbivores when there is only one phytoplankton species.

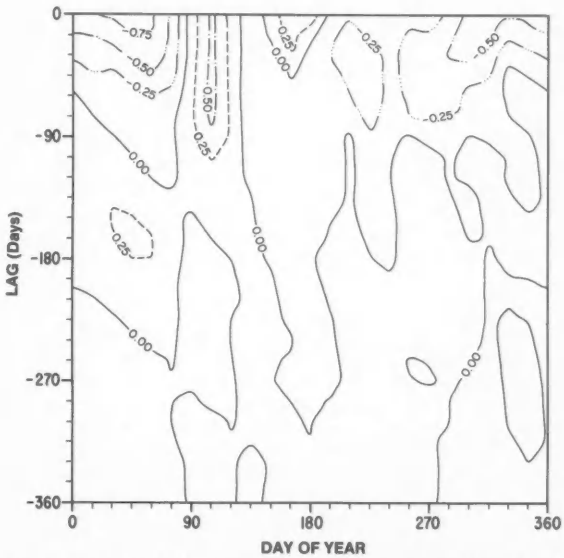

FIG. 6. Contours of τ for phytoplankton, for the same model as Fig. 5.

all parameter sets. Herbivore biomass is most variable in spring, and highest on average in summer (Fig. 2). There is a strong negative correlation with mid-autumn mixed layer depth that lasts from zero lag (contemporary) through the following 6 mo (Fig. 3). ($\tau = -0.5$ means that, for any pair of years, the year with the shallower mixed layer has the higher herbivore concentration 75% of the time.) Herbivores in winter and spring are positively correlated with mixed layer depth the previous summer. The positive correlation with the previous summer is generally weaker, but longer lasting, than the negative correlation with the previous autumn. Herbivores in spring are only weakly correlated with contemporary (or any other) mixed layer

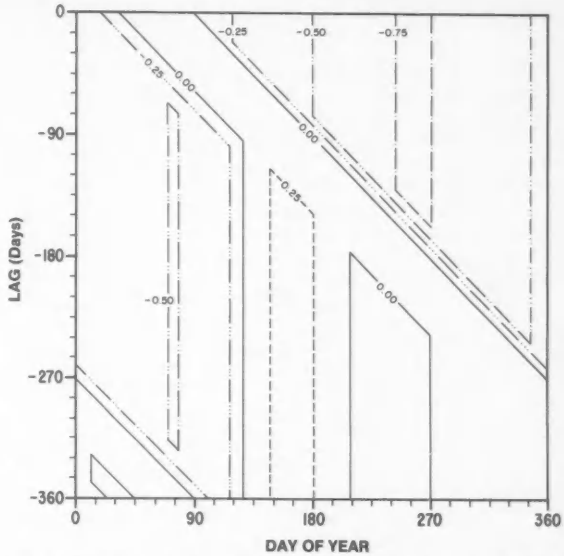

FIG. 7. Contours of τ for herbivores when only the summer mixed layer depth varies.

depth, possibly because they are affected by competing influences. Although the assumptions of linear regression are probably not met, Fig. 4 shows r^2 for the same data: contemporary mixed layer depth explains over 60% of the variation in autumn herbivores, and there is no variable that explains a large part of the variation in spring herbivores.

We also tried assuming that a constant fraction of the mixed layer, rather than a constant number of metres, was replaced each day by mixing. This makes the mixing rate greater in winter when the mixed layer is deep. We found that it made little difference to the predictability.

Possible Causes of Low Predictability

We have asserted that more complicated models are harder to predict. If this is true, then the model with only one type of phytoplankton should be more predictable. In support of this, Evans (1988) found that even with an annually repeating cycle of mixed layer depths, a model with two phytoplankton species can have more complicated behaviour, including biennial or even aperiodic cycles, than a model with ony one. We therefore deleted the summer (Q) phytoplankton species, and found the τ's of Fig. 5. The relation with contemporary mixed layer depth is indeed improved for most of the year, but still not for early spring. We note in passing that although phytoplankton are more directly affected by mixed layer depth than herbivores are, both are about equally predictable (equal values of τ). Comparing Figs. 5 and 6, in early spring phytoplankton is more predictable than herbivores, but throughout the rest of the year herbivores are more predictable. This supports our contention that causal relations are subtly distributed by population dynamic processes, and that the search for immediate relations is likely to be fruitless.

The change between years in the pattern of mixed layer depths is described by six numbers, and it is therefore possible that our problems arise from trying to predict too much from a single number, such as average mixed layer depth in early summer. To explore this possibility, we created a hypothetical history in

which only the depth of the summer mixed layer varied between years; all other depths and timings were held constant at their average values. The results (Fig. 7) are similar to when all six descriptors vary (Fig. 3). The apparent orderliness of the figure is an artifact: the mixed layer depths (independent variables) that vary between years are all perfectly correlated with each other.

Although the analysis we performed is well suited to the sorts of observations that are likely to be available, our simulated observations are much more frequent and it might seem reasonable to perform a more detailed time series analysis. This is not easy, because the series is seriously nonstationary. The mean and the variance of herbivores are much lower in winter than at other times of year, and even if we transform the series to have constant mean and variance, there is no reason to suppose that doing so will produce a constant correlational structure. Spectral analysis therefore seems like a poor bet. We performed such an analysis for one parameter set ($N_0 = 9$, $m = 1.8$), and confirmed that it wasn't informative: regardless of transformations or the degree of spectral smoothing, we found no significant squared coherence except at annual periods. This could have been predicted from Fig. 3: the correlation at any lag clearly depends on the time of year, so that analyses that assume stationary series cannot be appropriate (Transformation to constant mean and variance will of course not affect rank order correlations.)

Discussion

Plankton

Some of the suggestions of Evans and Parslow (1985) for exactly periodic models are confirmed here for aperiodic models in which cause and effect can be separated. Late summer and early fall herbivores are well predicted by contemporary mixed layer depth. This is consistent with comments in Evans and Parslow (1985) that the model is near its equilibrium for that time of year. The mixed layer depth in spring turned out to be the worst predictor for both phytoplankton and zooplankton, and the mixed layer depth in summer is a fair predictor for the following spring. This is not what would have been expected from Sverdrup (1953), but it is consistent with the conclusion of Evans and Parslow (1985) that the spring bloom is a consequence of the system deviating from equilibrium in the previous winter.

This exercise has implications for long-term global models of plankton ecosystems. One wishes to keep these models simple, partly to save computer time, and partly because the supporting data from satellites will not soon be able to distinguish different species groups. Our results, and especially a comparison of Figs. 3 and 5, suggest that food chain models of the ocean, derived from measures of chlorophyll rather than phytoplankton types, will probably overestimate its predictability.

The model is for a self-contained body of water, whereas the time series is taken from a location in an ocean current. A more correct model would include horizontal transport of the plankton, which would therefore be in different latitudes in different years; but it seems unlikely that the time series of mixed layer depth history with changing position needed to drive such a model will soon be available.

Fish

Although fish larvae are present at almost any time of year, they are most abundant in spring and early summer (Russell 1976; Markle and Frost 1985). This is therefore when zooplankton are likely to be most important; it is also when they are most variable (Fig. 2) and least predictable (Fig. 3). If recruitment success depends on the timing and density of herbivores, it may therefore be hard to predict from environmental signals. It is often suggested that variation in planktonic food helps determine larval survival (reviews in Lasker 1981; Rothschild 1986), but direct field evidence is poor (Leak and Houde 1987; Rice et al. 1987; Taggart and Leggett 1987). It thus appears that both links in the chain of prediction from environment to plankton concentration to larval survival are weak.

Although we postulate effects of zooplankton concentration on fish larvae, our model does not include any feedback effects of larvae on the plankton. This is reasonable if fish larvae do not occur in concentrations dense enough to affect other plankton populations. This assumption is consistent with Cushing (1983) and Taggart and Leggett (1987), although not with Jones and Hall (1974).

The herbivores are modelled as biomass, with no internal size structure, whereas fish larvae feed primarily on copepod eggs and nauplii. Jones and Hall (1974) and Ware (1977) have suggested that fish may be adapted to releasing their eggs at times when prey of suitable size are more abundant rather than when overall biomass is high. Frank and Leggett (1986) demonstrated that potential significance of this strategy using in situ experiments. A model that takes account of the life history of herbivores would be a useful refinement, although there is no reason to expect it to be any easier to predict.

High average concentrations, low variability, and high predictability are all qualities of herbivore biomass that fish would find desirable. They do not all occur at the same time of year; the time of highest predictability and lowest inter-annual variability is also the time of lowest average biomass. This suggests the possibility of r versus k recruitment. Fish species with low but unvarying recruitment might have their early larval period in late summer; species with high and variable recruitment might have theirs in the spring. It might also happen that eggs produced at an unpredictable time of year tend to be larger (P. Pepin, unpubl. data).

There is a consistent indication that herbivores can be predicted to some degree from the previous early summer's mixed layer depth. This is interesting, because the early summer mixed layer depth could conceivably be used as a cue by adult fish, to influence their allocation of energy to gonadal growth based on the conditions their larvae might encounter — the prediction would be far from perfect, but perhaps usefully better than random over evolutionary time. There is evidence that the quantity and quality of herring eggs is correlated with environmental conditions up to 6 mo prior to the spawning period (Tanasichuck and Ware 1987).

Correlations between environment and recruitment might be high for reasons unrelated to the local ecology discussed here. Advection of larvae into suitable or unsuitable areas is often considered to be important in determining year-class success (Nelson et al. 1977; Bakun and Parrish 1980; Bailey 1981), and fluctuations in transport are likely to be correlated with fluctuations in other physical variables like temperature or mixed layer depth.

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Bacteria–Organic Matter Relationship in Sediments: A Case of Spurious Correlation[1]

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Bird, D. F. and C. M. Duarte. 1989. Bacteria–organic matter relationship in sediments: a case of spurious correlation. Can. J. Fish. Aquat. Sci. 46: 904–908.

A longstanding claim regarding the existence of a strong positive relationship between bacterial abundance and organic matter in aquatic sediments is shown to be potentially spurious. The statistical significance of the relationship results primarily from standardization of both variables to dry weight of sediments. We suggest that other published relationships may be similarly artifactual. Deceptive results are possible unless standardization is done with caution.

Depuis longtemps certains prétendent qu'il existe une corrélation fortement positive entre l'abondance des bactéries et la teneur en matières organiques dans les sédiments aquatiques, mais on a démontré que cette corrélation pouvait être illusoire. La signification statistique de la corrélation provient essentiellement de la normalisation des deux variables en fonction du poids sec des sédiments. Nous avons proposé que d'autres corrélations mentionnées dans les publications pouvaient également être fausses. On peut s'attendre à des résultats illusoires à moins que la normalisation ne soit effectuée avec prudence.

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The initial approach to understanding a complex ecological system is often, sensibly, to look for general quantitative relationships between two or more variables describing the system (Rigler 1982). This search is not done blindly, but proceeds on the basis of previous successes in other systems and logical connections between the variables of interest. Thus in his approach to the problem of sediment microbiology, Dale (1974) showed that highly significant relationships exist between bacterial abundance and both organic matter content and sediment grain size of marine intertidal sediments. Dale suggested that the correlation with grain size was due to a greater surface area in fine than in coarse sediments, but that the correlation with organic matter could not be assigned to a causal connection without some measure of the nutritive quality of the organic matter. Rublee (1982) reviewed the literature on sediment bacteria and showed that the relation with organic matter was quite general, and fit a broad range of data from estuarine sites.

More recently, Yamamoto and Lopez (1985) confirmed that bacterial abundance in intertidal sediments was strongly related to surface area using directly measured surface area per gram dry weight of sediment. On the strength of this relationship, those authors suggested that density-dependent processes related to particle surface area controlled bacterial numbers. Bott and Kaplan (1985) extended the analysis to freshwater and suggested, on the basis of multiple regression analysis, that bacterial biomass in stream sediments may be more strongly related to sediment particle size, representing surface area for colonization, and organic matter content of the sediment, representing either surface area or nutrient source, than to organic substrates in the stream water. Since particle size and organic matter per gram dry weight of sediment were themselves correlated ($r = -0.78$, $p < 0.001$), the two effects could not be differentiated. Finally, a comparison of three different methods for measuring microbial activity in stream sediments (Baker 1986) showed that all methods were closely correlated to each other, and that microbial activity was correlated to sediment organic matter content and bulk density, but not to either stream flow or sediment temperature.

This paper will show that all of the above relationships may be largely spurious, and that the conclusions based on them will require reexamination.

When a correlation is termed spurious, we mean one of two things. First, a correlation is spurious if its statistical significance depends on an unidentified tautological relationship between two variables or their components and not on any true empirical informative content. Second, a correlation is spurious if its significance is inflated by an unsuspected, albeit nontautological, correlation between variables and variable components. The 'spurious' aspect of a spurious correlation refers not to the correlation itself, but rather to the improper attribution of the strength of the overall relationship to variable subcomponents. In particular in the present case, correlations between ratios with different numerators but the same denominator are not automatically improper; the danger lies in ascribing the strength of the relationship to the numerators alone (cf. Kuh and Meyer 1955). How these definitions apply in the present case will come out most clearly by example.

Materials and Methods

Since the raw data needed to prove our point were not provided by any of the studies listed, we will use only the data

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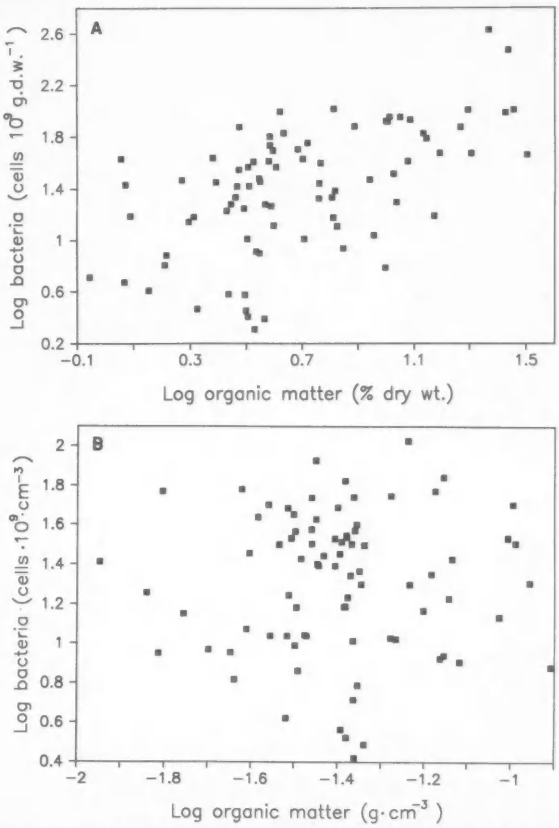

FIG. 1. (A) Scatter plot of the relationship between bacterial abundance (per weight dry sediment) and organic matter (per weight dry sediment) in the littoral zone of Lake Memphremagog, Quebec–Vermont, July–August 1984. (B) Scatter plot of the same relationship expressed per volume of sediment.

collected as part of our own study (Duarte et al., unpubl. data). Protocols for relevant variables are repeated here for convenience. Sediment and macrophyte samples were collected by SCUBA divers during July–August 1984 at 56 sites in mesotrophic Lake Memphremagog, Quebec–Vermont. Some sites were visited more than once, so that 80 samples complete in all measurements were collected. Duplicate sediment core samples (5 cm internal diameter) were collected at each site. The upper 5 cm of sediment was extruded from each core, and the two cores were amalgamated and hand-stirred. A 2-g sample was made up to 50 ml with 0.2-micrometre-filtered lake water. Formalin was added to a final concentration of 5%, the suspension was vigorously shaken and a 1 ml subsample was taken and diluted to 20 ml with filtered distilled water containing formalin. This suspension was sonified in emulsifier and Vortex-mixed for 10 min. A 2-ml subsample was withdrawn for epifluorescence enumeration of bacteria (Porter and Feig 1980; Coleman 1980), yielding an estimate of bacterial abundance per gram fresh weight.

A subsample of the upper 5 cm of the sediments was dried to constant weight at 110°C, then burned overnight at 550°C, to determine the water content (percent fresh weight) and organic matter content (percent dry weight) from mass loss. Bacterial and organic matter content per unit weight of sediment were transformed to content per unit volume of sediment using bulk density estimates based on an equation relating bulk density (grams per cubic centimetre) to water content (WC: percent fresh weight) and organic matter (OMW: percent fresh weight) (Hakanson and Jansson 1983, p. 82):

$$\text{Bulk density} = 260/(100 + 1.6(\text{WC} + \text{OMW})).$$

The equation assumes that the densities of water and organic matter are 1.0 g·cm^{-3} and of inorganic matter is 2.6 g·cm^{-3}. Measured densities of silt, clay, and sand range only from 2.60 to 2.85 g·cm^{-3} (Hakanson and Jannson 1983, p. 82) whereas the inorganic matter concentration in the sediments of Lake Memphremagog ranged from 0.08 to 2.02 g·cm^{-3} of sediment. Therefore slight errors in the estimation of bulk density would be unimportant. All data used in this study are available at nominal cost from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2.

Results and Discussion

First, we too found a significant positive relationship between bacterial abundance and organic matter per gram dry weight. The relationship was similar in form to that reported by Rublee (1982) (Fig. 1a, Table 1) though significantly weaker (F-test, $p < 0.05$). However the relationship broke down when expressed per unit volume (or area) of sediment (Fig. 1b, Table 1). This was initially thought to be a consequence of the well known positive correlation between water content and organic matter content of sediments (Hakanson and Jansson 1983, p. 80), such that the true increase in bacterial abundance in organic rich sediments was obscured by the concomitant dilution of such sediments with water. It was also possible, however, that the significance of the dry weight relationship was being affected by the "standardization" of all measurements to dry weight units of sediment (Fig. 2). The possibility was tested by examining whether the disruption of existing relationships between the variables affected the significance of the dry weight based relationship. To do this, corresponding estimates of bacterial abundance (cells per cubic centimetre) and organic matter concentration (grams per cubic centimetre) were divided by randomly reassigned measurements of dry weight (grams per cubic centimetre) to reestablish pairs of bacteria–organic matter measurements per gram dry weight. A new regression equation based on these reshuffled data could then be calculated and compared with the original unmodified equation. This scrambling procedure did not affect the strength of the relationship. One hundred and forty out of 1000 equations based on reshuffled data had slopes larger than the original (Fig. 3). Similarly, when all three variables were randomly shuffled and rejoined, the slopes of the regression equations between them were indistinguishable from the one observed with the original data.

The significance of a regression equation rests on a standard test of the departure of the slope of the equation from a null hypothesis value of zero. In the case just outlined, the slope cannot be made insignificant even by complete randomization of the data, since its significance rests entirely on the dry weight factor in the denominator of both variables. The dry weight factor provides the correlation; bacteria and organic matter provide only the scatter in the relationship.

An alternative analytical approach to the data verifies the above analysis. When it is suspected that an extraneous variable

TABLE 1. Regression equations between sediment parameters. All variables transformed to logarithms. Units are per cubic centimetre (vol) or per gram dry weight (g dw). Bacteria in billions of cells, other variables in grams. ns = not significant at $a = 0.05$, * = data from Rublee (1982), RMS = residual mean square.

Dependent variable	Independent variable	Slope	r^2	RMS	n
Bacteria (g dw)	Organic matter (g dw)	0.74	0.31	0.165	80
Bacteria (vol)	Organic matter (vol)	0.03	0.00ns		80
Water (g dw)	Organic matter (g dw)		0.67		80
Water (vol)	Organic matter (vol)		0.09		80
Bacteria (g dw)	Organic matter (g dw)	0.90	0.83	0.10	114*
Bacteria (g dw)	dry weight (vol)	−0.59	0.75		32*
Bacteria (vol)	dry weight (vol)	−0.27	0.12ns		32*

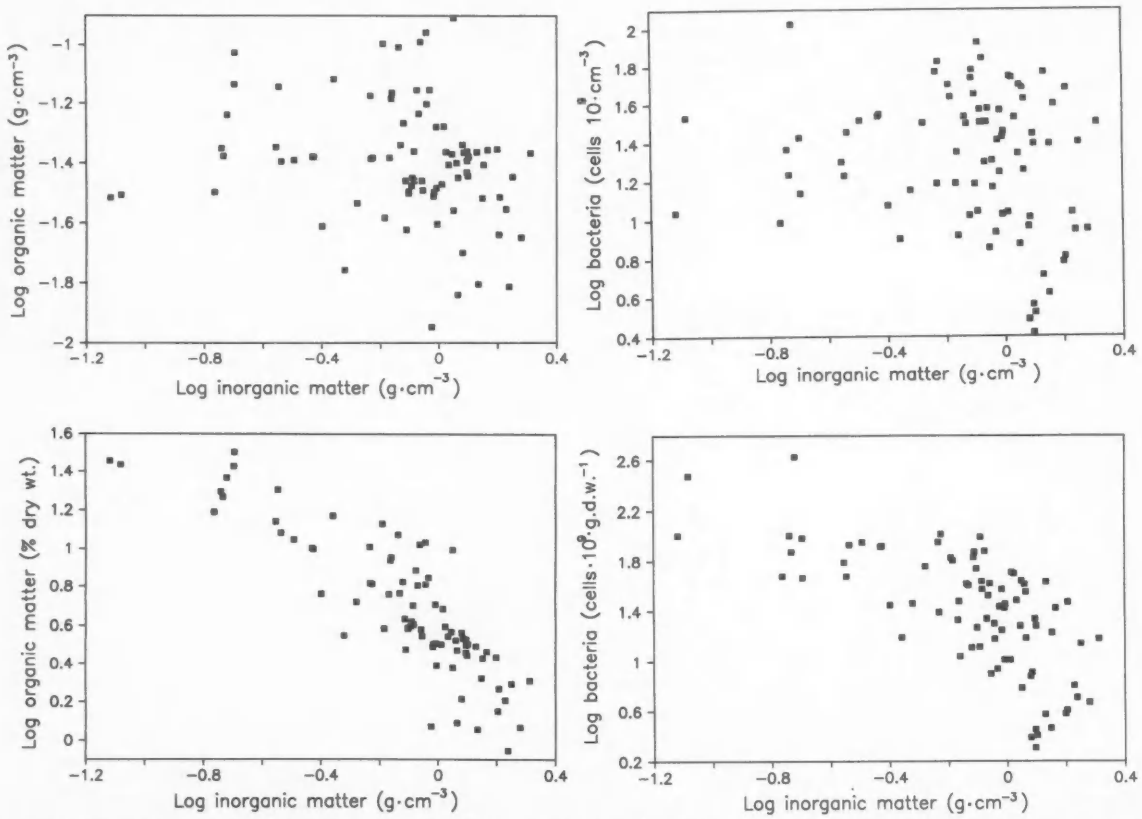
Log organic matter (g·cm⁻³)
Log inorganic matter (g·cm⁻³)
Log bacteria (cells 10⁹·cm⁻³)
Log inorganic matter (g·cm⁻³)
Log organic matter (% dry wt.)
Log inorganic matter (g·cm⁻³)
Log bacteria (cells·10⁹·g.d.w.⁻¹)
Log inorganic matter (g·cm⁻³)

FIG. 2. Scatter plots of organic matter and bacterial abundance versus sediment inorganic matter. Upper panels are expressed per unit sediment volume; organic matter and bacterial abundance in lower panels are expressed per gram dry weight. The improvement in the relationships in the lower panels is due solely to "standardizing" to gram dry weight units.

(in this case, sediment bulk density) is influencing the "absolute" measures of interest, partial correlation or regression analysis can be used to screen out the interference. The simple coefficient of determination (r^2) between bacteria and organic matter per gram dry weight was 0.31 (Table 1). The partial coefficient of determination controlled for differences in dry weight per volume was less than 0.001; controlled for differences in inorganic matter per volume, it was 0.002. Therefore, it is mistaken to suggest that a strong relationship between bacterial abundance and organic matter per gram dry weight results from an influence of organic matter on bacteria or says anything at all (by itself) about bacteria–organic matter relationships in the sediments.

Another form of spurious correlation involving variables expressed per gram dry weight occurs when the opposite variable is itself correlated with sediment bulk density. An example is the relationship between bacterial abundance per gram dry weight and nearby macrophyte biomass. There is a weak though significant (and genuine) relationship between bacteria per sediment volume and macrophyte biomass within a 50-cm radius of the cored site (Fig. 4). The strength of the relationship is increased by expressing the bacteria per gram dry weight

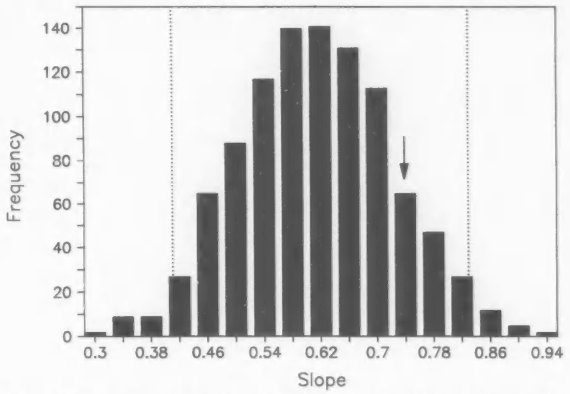

FIG. 3. Frequency distribution of 1000 regression slopes relating sediment bacterial abundance (10^9 cells·g dry weight^{-1}) and organic matter concentration (OM) (g·g dry weight^{-1}). To produce these slopes, corresponding measurements of bacteria (cells·cm^{-3}) and OM (g·cm^{-3}) were divided by randomly reassigned measurements of dry weight (g·cm^{-3}). Arrow shows the observed slope of the original measurements. Dotted lines represent the 2.5 and 97.5 percentiles. There was no difference between the slope of the observed relationship and those of the randomly reassorted data, and all reassorted data slopes were significantly greater than zero ($n = 80$).

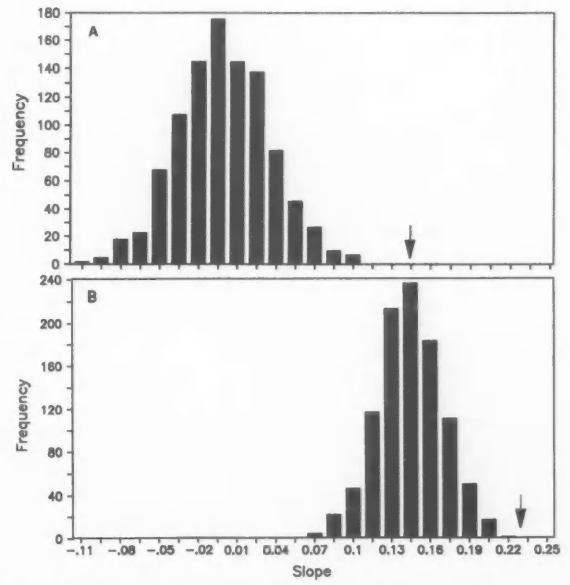

FIG. 4. Frequency distributions of 1000 regression slopes between bacterial abundance and macrophyte biomass. (A) Bacterial abundance per volume of sediment was randomly reassorted and regressed against macrophyte biomass. The observed slope (arrow) of the original data falls outside the curve ($p < 0.001$). (B) Bacterial abundance per volume divided by randomly reassorted dry weight per volume, regressed against macrophyte biomass. The observed slope (arrow) of the unrandomized data also falls outside the curve ($p < 0.001$). The difference between the observed slope in (A) and the observed slope in (B) is due to the correlation between macrophyte biomass and sediment dry weight per volume.

(Fig. 4). Monte Carlo randomization revealed that this increase is due to an additional weak, significant, and nonspurious negative correlation between macrophyte biomass and dry weight per volume of sediment. The danger in this situation is of an uncritical attribution of the correlation entirely to the bacteria–macrophyte relationship. We believe that such spurious inference may occur for relationships between bacteria per gram dry weight and sediment particle size. Though not obviously deceptive, such relationships depend heavily on the documented (e.g. Hakanson and Jansson 1983, p. 92) positive correlation between particle size and sediment bulk density. The particle size–bulk density relationship is even stronger in Lake Memphremagog littoral sediments than is the bulk density–organic matter relationship (E. Petticrew, McGill University, pers. comm.).

Although the practice of expressing sediment parameters per gram dry weight is standard in the literature (Hakanson and Jansson 1983, p. 67), the uncritical use of dry weight units should be reconsidered. There are contexts where gram dry weight or allied units are appropriate, such as when giving concentrations of sediment contaminants that are quantitatively bound to a particular size fraction of the dry material (Forstner and Salomons 1981, cited in Hakanson and Jansson 1983, p. 66). One should be aware, however, that loading calculations require volumetric or areal units. Furthermore, biological activity per gram dry weight has little meaning in the absence of corresponding data on water content and bulk density, and these should always be supplied. Note that we are arguing for the conceptual and practical priority of volumetric (areal) units over dry weight units: neither is an absolute measurement.

If it is suspected that dry weight per volume of sediment is itself important to the bacteria, of itself or as a surrogate for an unmeasured variable, then dry weight can be included as an additional independent variable in a multiple regression analysis. This is equivalent to calculating the partial correlation coefficient, controlling for changes in sediment bulk density. Comparison of means of samples between sites or times would be carried out by analysis of covariance, with dry weight or inorganic matter content as the covariate.

Unfortunately, the conclusions based on the methodologically biased aspects of the studies cited in the introduction must be reassessed in light of the present findings. The conclusions may yet prove to be justified, though in a modified form. For instance, a recent study has shown that there is indeed a positive correlation between bacterial abundance per square metre and organic matter per square metre in Georgian blackwater river sediments (Findlay et al. 1986). On the other hand, the "basically simple relation between surface area, organic content, and the size and metabolism of communities of microorganisms associated with aquatic sediment" envisioned by Hargrave (1972) may have to give way to one less satisfying and more complex. Factors already shown to influence sediment bacterial abundance or activity include grazing by macroinvertebrates (Moriarty et al. 1985), primary production by microphytobenthos (Meyer-Reil et al. 1980; Findlay et al. 1986), particle suitability for colonization (DeFlaun and Mayer 1983; Yamamoto and Lopez 1985), sediment redox potential (Jones 1982), sediment temperature (DeFlaun and Mayer 1983), quality and quantity of water column dissolved organic carbon (Bott and Kaplan 1985), interaction between macrobenthos and detritus supply rates (Alongi and Hanson 1985), and proximity to growing macrophytes (Duarte et al. 1988). Future studies will show which among these factors are most consistently important.

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